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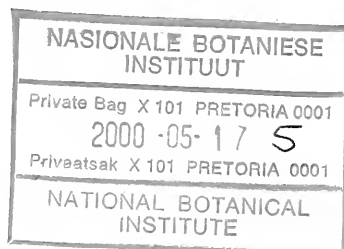
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Notes on the genus *Frithia* (Mesembryanthemaceae) and the description of a new species, *F. humilis*, in South Africa

P.M. BURGOYNE*, G.F. SMITH* and F. DU PLESSIS**

Keywords: *Frithia* N.E.Br., Mesembryanthemaceae, new species, South Africa, summer rainfall mesembs, taxonomy, window plants

ABSTRACT

Frithia N.E.Br. (Mesembryanthemaceae), formerly thought to be a monotypic genus, has been found to comprise two species. Populations from the eastern parts of the distribution range of *Frithia pulchra* N.E.Br. are recognised as a distinct species, *Frithia humilis* P.M.Burgoyne. The genus has a limited distribution, although present in three provinces of South Africa, namely Gauteng, North-West and Mpumalanga. The two window-leaved species are allopatric and morphological differences between the roots, leaves, flowers, pollen, capsules and seeds are discussed. A formal description of the new species, an identification key and a distribution map of the two species are provided.

INTRODUCTION AND HISTORICAL OUTLINE

The genus *Frithia* (N.E.Br.) was first mentioned in a key by Brown (1925). At that time no species were assigned to the genus and only later was a full description of *Frithia pulchra* given (Brown 1926). The genus was named after Frank Frith (1872–1954), a railway services gardener stationed at Park Station, Johannesburg. He was responsible for decorating railway platforms from 1900 until his retirement in 1932 (Kroon 1997). In 1906, Olive Nation sent a specimen of a plant she discovered near Rustenburg to Brown at Kew for identification. The live specimen did not survive the journey, but the remains were seen by Brown who regarded it as a distinct entity. After Miss Nation died, a search for more material proved unsuccessful. Some time later, a Mrs Dobie of Rustenburg sent plants to Frank Frith, who took the specimens to Brown at Kew while on a visit to London, to create the African garden at the Wembley Exhibition. Dobie's specimen allowed Brown to finally describe the genus.

De Boer (1968) published the name *Frithia pulchra* var. *minor* in the Dutch journal *Succulenta*, but as no type material was cited the name was invalid. Plants of this variety are generally smaller than those included in var. *pulchra* and are restricted to the eastern parts of the distribution range of the genus. These differences were again alluded to by Hardy & Fabian (1992). Zimmermann (1996) confirmed the different characters of var. *minor*, but gave no formal description or type validating the varietal epithet. Although a number of short articles have been written on *Frithia* (Brink 1985; Germishuizen 1975; Steffens 1988; Venter 1979, 1983), no in-depth study has been done on the genus.

This paper reports on the taxonomic status of the genus, and specimens from the eastern parts of its distribution range are formally described as a new species, *Frithia humilis*.

TAXONOMY

To prevent possible confusion with the illegitimate name *Frithia pulchra* N.E.Br. var. *minor* de Boer, the varietal epithet *minor* is not used at the specific rank. The name of the new species is derived from the Latin *humilis*, which means 'smaller than others of its kind'.

Key to species

- Window of leaf tips convex with no markings along margins; leaves 15–25 mm long, blue-green or grey-green; flowers bright magenta with gold, yellow or white centre, 25–35 mm diam.; growing west of Pretoria in the Rustenburg area 1. *F. pulchra*
- Window of leaf tips concave with crenulate markings along margins; leaves shorter than 15 mm, brown-green or dull green; flowers white with yellow centre, pale pink, rarely entirely pink, petals sometimes tipped with pale pink, 15–20 mm diam., when pollinated turn pale yellow or salmon-orange; growing east of Pretoria in the vicinity of Bronkhorstspuit and Witbank 2. *F. humilis*

Frithia humilis P.M.Burgoyne, sp. nov.

Frithia pulchra N.E.Br. var. *minor* de Boer: 147, 148 (1968), nom. illeg.

Plantae perennes nanae succulentae, radicibus succulentis lateraliter ramosis, tempore mensium hibernium in humum arenosum retractae per foliis contractilibus longitudinaliter vietiis fiunt praesentia eorundum cavis relictis indicata. *Caulis* simplex, brevis, ad 10 mm longus. *Folia* spiraliter disposita, obscure virides ad brunneo-virides, mensis aridis hibernis purpureo-suffusa, maxime succulenta, ad 15 mm longa, cylindrica, idioblastis ceraeis distincte serialibus, apicibus foliorum fenestratis cum centro concavo, maculisque conspicuis crenulatis perimetro. *Flores* solitaires, 15–20 mm diametro, albi vel perdilute rosei, centro flavo, ante ad post meridiem aperiens. *Sepala* 5, inaequalia, folia simulantia, tubum brevem connata. *Petala* 20–30, in verticillis plures disposita, apices plerumque acuminati, interdum rotundati. *Staminodia* petaloidea ad filiformia, verticillos aliquot staminum cingentia. *Hypanthium* basibus connatis petalorum staminodium staminumque formatum. *Necta-*

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ria 5, libra, atroviridia, crenulata. *Ovarium* supra leviter conicum, stigmata 5 vel 6, perbrevia. *Fructus* capsula 5-vel 6-locularis, doliiformis, perfragilis, maturitate rumpens, semina spargens; valvae ad positionem erectam aperientes, alae valvarum absentes, margines valvarum recurvati ubi omnis aperti, cristae turgescentes pallide luteo-brunneae, apicibus divergentibus marginibusque scissis, membranae tegentes ad regulam reductae. *Semina* rubro-brunnea, parva, tuberculis parvis tecta. Florescentia a Decembri ad Februarium.

TYPE.—Gauteng, 2528 (Pretoria): Bronkhorstspuit Dist., 29 km northeast of Bronkhorstspuit on tarred road to Verena, then 3 km along road to Susterstroom, on Farm Susterstroom, in sandy flat areas associated with rough rocky outcrops, (–BD), *Burgoyne* 6693 (PRE, holo.).

Perennial, dwarf succulent with fleshy roots branching laterally; plants retracting into sandy soil by means of contractile leaves shrinking lengthways during dry winter months, leaving holes marking their presence. *Stems* single, short, up to 10 mm long. *Leaves* arranged spirally, dull green to brown-green with a purple tinge in dry winter months, highly succulent, up to 15 mm long, cylindrical, covered by waxy idioblasts arranged in distinct rows, tips windowed, with concave centre and conspicuous crenulate markings along perimeter. *Flowers* single, 15–20 mm diam., white or very pale pink, with yellow centre, opening during mid-morning to mid-afternoon. Pollinated flowers turn yellow or salmon-orange. *Sepals* 5, unequal, resembling leaves, united to form a short tube. *Petals* 20–30 per flower, arranged in several whorls, tips mostly acuminate, sometimes rounded. *Staminodes* petaloid to filiform, surrounding several whorls of stamens. *Hypanthium* formed by fused bases of petals, staminodes and stamens. *Nectaries* 5, free, dark green, crenulate. *Ovary* slightly conical above; stigmas 5 or 6, very short. *Fruit* a capsule, 5- or 6-locular, barrel-shaped, very fragile, breaking up when ripe and then dispersing seeds; valves opening to an upright position, valve wings absent, valve margins recurved when fully open; expanding keels light yellow-brown, parallel, with diverging tips and torn margins; covering membranes reduced to a ledge; closing bodies absent. *Seeds* red-brown, small, covered by small tubercles. *Flowering time*: December–February (summer in the southern hemisphere).

As the formerly monotypic genus *Frithia* now has two species, the type species of the genus is *Frithia pulchra* N.E.Br.

SPECIMENS EXAMINED

All specimens held at PRE.

Burgoyne 6692, 6693, 6694, 6694b, 6696, 6698, 6699 (2), 6699b, 6699c (1).

Crundall PRE54981 (2).

Dyer 4774 (1). *Dyer & Verdoorn* 3922 (1).

Gillfillan 7272 (2).

Jacobsen 758 (1).

Rose Innes 167 (1).

Vari PRE54978 (1). *Venter* 2997 (2).

Young 38395 (1).

DISTRIBUTION AND HABITAT

Frithia is one of the few genera in the Mesembryanthemaceae exclusive to the summer rainfall region of South Africa. Other mesemb genera with a distinctly summer rainfall distribution include *Neohenricia*, *Mossia* and *Khadia*, while *Delosperma*, *Hereroa*, *Lithops*, *Chasmatophyllum*, *Nananthus* and *Stomatium* may occur in summer rainfall areas but also have wider distributions.

Previously thought to be a monotypic genus and a Magaliesberg endemic, an enlarged *Frithia* still has a restricted distribution. Populations of these miniature window plants have been found in two disjunct regions, in the North-West between Rustenburg and the Hartbeespoort Dam in the west, and in an area between Bronkhorstspuit (Gauteng) and Witbank (Mpumalanga) in the east (Figure 1). The two areas are roughly 150 km apart, and so far, no specimens of either species have been collected in the intervening area.

Both species of *Frithia* grow in very shallow soils derived from coarse sediments: quartzites of the Magaliesberg Formation of the Pretoria Group of the Transvaal Supergroup in the case of *Frithia pulchra* and sandstones of the Irrigasie Formation of the Eccia Group of the Karoo Supergroup for *F. humilis*. Rocks in both areas are very rough, porous and weather to form a very coarse gravel.

Frithia pulchra mostly grows exposed on rock plates, the roots anchored in cracks between the coarse quartzites. This substrate reaches very high temperatures in summer. Plants are also found in coarse gravel and are not restricted to rocky outcrops. *F. humilis* grows predominantly in shallow sand along the rims of large, flat, rock plates. Temperatures of the substrate are probably lower as more organic matter is present, insulating the plant bodies against heat and desiccation.

Both species grow at altitudes ranging from 1 368 m to 1 616 m, and rainfall varies between 700 and 800 mm per annum. Winters are cold and dry and severe frost occurs in the areas where the plants grow.

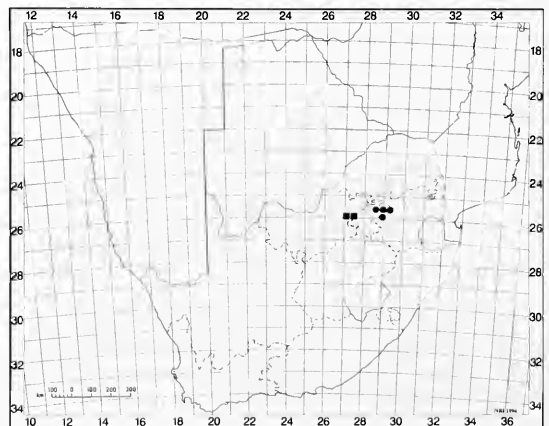


FIGURE 1.—Known distribution of *Frithia pulchra* ■, and *F. humilis*, ●.

Other species often associated with both species of *Frithia* are the fern ally *Selaginella dregei* and the legume *Indigofera melanadenia*. Species sometimes found associated with either species of *Frithia* are the succulents *Anacampseros subnuda* subsp. *subnuda*, *Crassula lanceolata* subsp. *transvaalensis*, *C. setulosa* var. *setulosa* and *Mossia intervallaris*. Monocots like *Microchloa kunthii*, *Anthericum calyptocarpum* together with an extremely minute and monophyllous species of *Drimia*, are also found in these habitats. The habitat of *Frithia pulchra* tends to be drier than that of *F. humilis*, the soils where the latter grow, having a higher organic content, sometimes resembling peat, and thus retaining moisture better.

FRITHIA IN HORTICULTURE

Frithia pulchra and *F. humilis* differ widely in their horticultural history. *F. humilis* was introduced to the Dutch seed trade by de Boer thirty years ago and a few of the plants dating from that introduction are still alive. This species is obviously quite tolerant and it responds to water more eagerly than does *F. pulchra*. The latter has been in continuous cultivation since the late 1920's but the plants are usually not long-lived, easily succumbing to rot. Both species can mature in a few months from seed under favourable conditions, and in this respect they are typical of a *Delosperma* alliance. The two species readily hybridize (S. Hammer pers. comm.) producing fertile offspring, with a variety of flower colours including orange and bright pink. Many attempts made by Hammer to hybridize *Frithia* with other genera (*Delosperma*, *Drosanthemum*, *Dorotheanthus*, *Lithops* and *Fenestraria*) have always failed, not even producing the 'dummy' (empty) fruits which often result from such disjunct liaisons.

MORPHOLOGICAL CHARACTERS

Habit

Both species are dwarf perennials with thickened roots. The stems are much reduced and during periods of drought the plants retract into the sandy soil. This has been ascribed to contractile roots, but no such roots are present in either species. However, in *Frithia* the cells of the leaves are arranged in columnar, axial rows and when moisture is lost and the cells shrink, the tangential walls contract. Artificially induced dessication using silica gel, indicated that a leaf may contract to up to one third of its length (Figure 2B). This causes the plants to retract into the soil, a mechanism which renders protection to the plants during times of drought (Figure 3C). Retraction into the ground is thus achieved by means of 'contractile leaves', not contractile roots.

Roots

Roots of *Frithia pulchra* differ from those of *F. humilis* in being more fibrous, possibly because of the drier conditions prevailing in its habitat and the strategy to insulate the plants against the heat of surrounding rocks in summer.

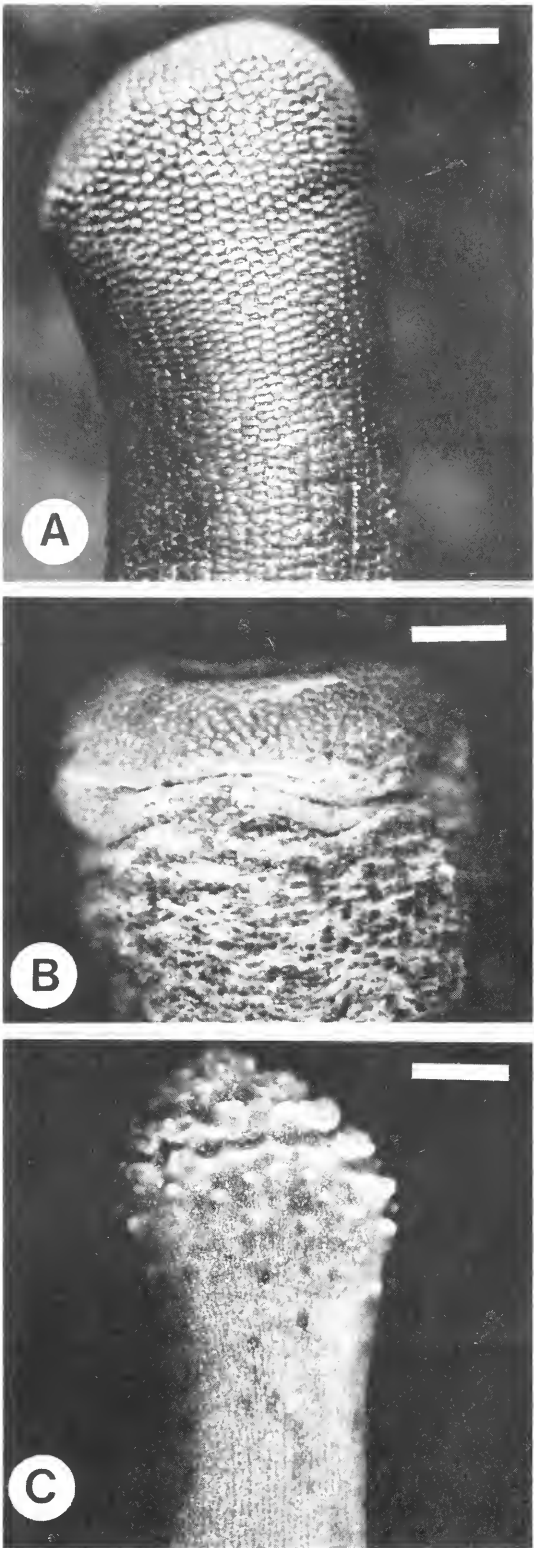


FIGURE 2.—*Frithia pulchra*: A, turgid leaf when conditions are favourable; B, shrunk leaf under drought conditions C, *Neohenricia sibbettii*, leaf. A, Burgoyne 6699c; B, Burgoyne 6694b; C, Burgoyne 6786b. Scale bars: 1 mm.

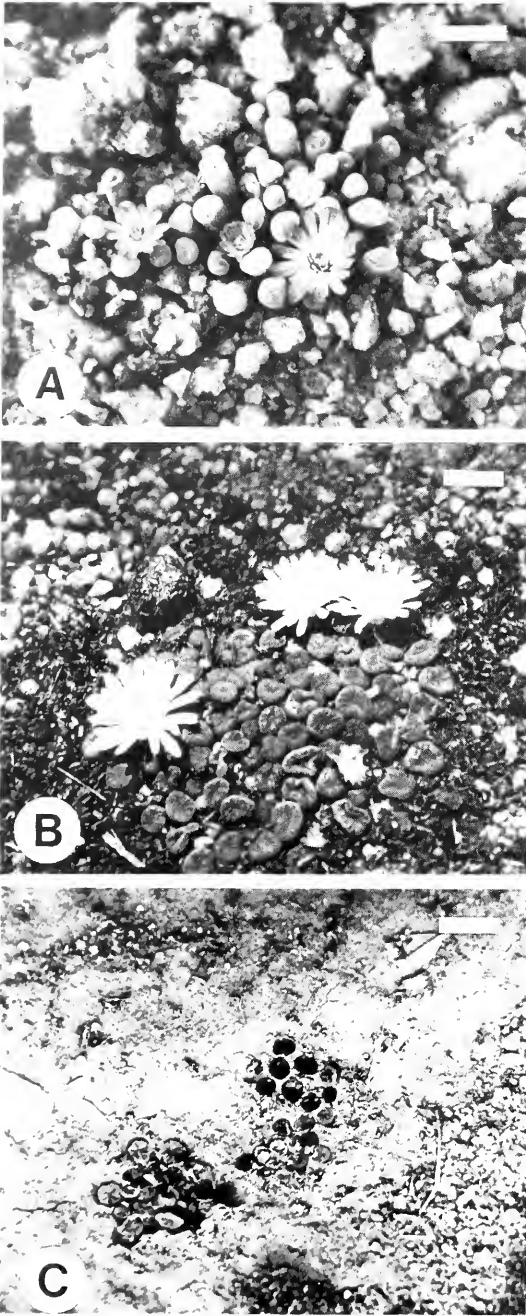


FIGURE 3.—Habit of *Frithia*: A, *F. pulchra*; B, *F. humilis*; C, plants of *Frithia humilis* retract underground during periods of drought. Scale bars: A, 10 mm; B, 30 mm; C, 10 mm.

Leaves

Borne spirally, the leaves of both species are cylindrical with windowed tips and are covered by an epidermal layer of waxy idioblasts arranged in distinct rows (Figure 2A). Leaves in adult plants of *F. pulchra* are longer (15–25 mm) than in *F. humilis* (shorter than 15 mm). Leaf colour also varies slightly between the two species, those of *F. pulchra* having a bluish tinge, whereas those

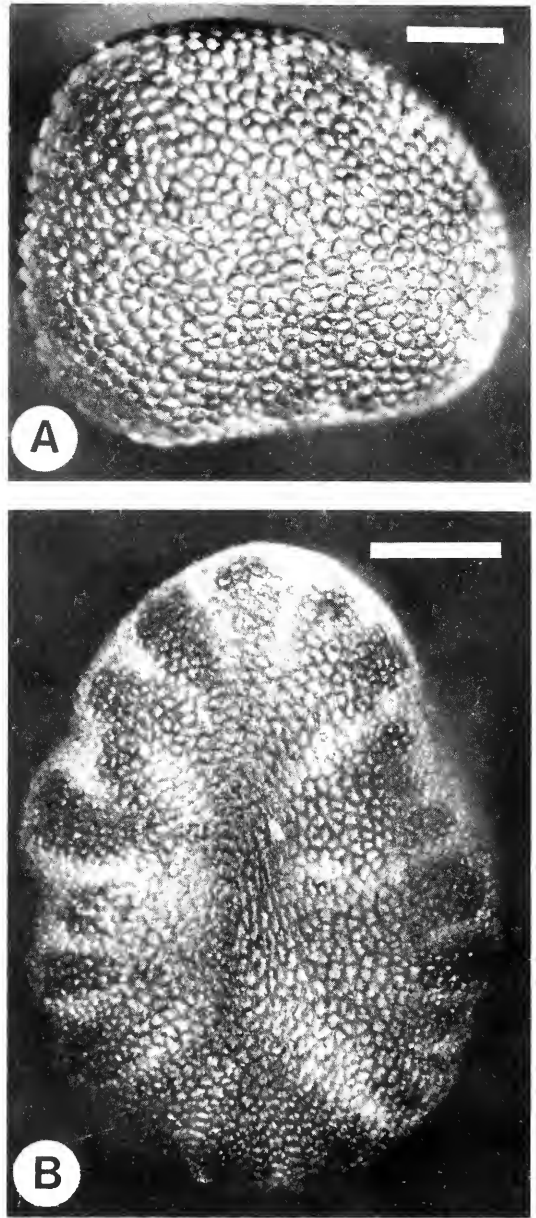


FIGURE 4.—Surface of leaf tips of *Frithia*: A, *F. pulchra* showing convex tips and no markings; B, *F. humilis* with concave centre and crenulate markings on margins. A, Burgoyne 6699c; B, Burgoyne 6694b. Scale bars: 1 mm.

of *F. humilis* are tinged brown or purple. The windowed tips of the leaves, however, differ conspicuously between the two species. Windows of *F. pulchra* are convex when turgid, slightly concave when flaccid (Figure 4A) and those of *F. humilis* are concave even when turgid, with crenulate markings (Figure 4B) along the margins. These leaf differences were also noted by Zimmermann (1996).

Flowers

Flowers in both species are borne singly and on very short stalks or are stalkless. They are subtended by five

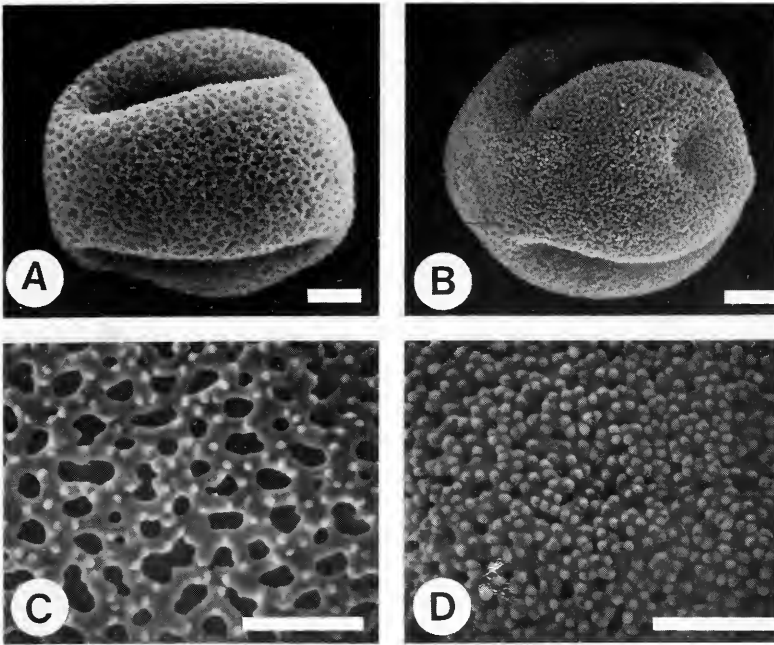


FIGURE 5.—Pollen of *Frithia*. SEM micrographs of unacetolyzed pollen grains: A, *F. pulchra*; B, *F. humilis*. Detail of pollen surface: C, *F. pulchra*; D, *F. humilis*. A, C, Burgoyne 6699c; B, D, Burgoyne 6694b. Scale bars: A, B, 1 μ m; C, D, 0.5 μ m.

unequal sepals closely resembling the cylindrical leaves. Flowers of *F. pulchra* are bright magenta with a white or light yellow centre and are 25–35 mm in diam. Those of *F. humilis* are white with a yellow centre, sometimes tipped with pale pink, and are generally smaller (15–20 mm diam.). The petals number between 30 and 45 in *F. pulchra* and tend to have blunt, rounded tips, whereas those of *F. humilis* number between 20 and 30 and usually have acuminate tips (Figure 3A, B).

Pollen

Pollen in both species of *Frithia* is yellow. The grains are tricolpate and simplicolumellate in *F. pulchra* (Punt *et al.* 1994) with a perforate surface and lumens of different sizes. Pollen in *F. humilis* has a perforate surface, and is pluricolumellate, with lumens of more or less equal size (Figure 5).

Fruit

Fruits are hygrochastic capsules, the shape resembling a barrel. Thick tissue surrounds the capsules of *F. pulchra*, whereas that of *F. humilis* is more fragile (Figure 6C). However, this character is not constant for the two species and seems to vary with environmental conditions. Capsules of both species tend to break up shortly after ripening. In both species, there are five or six locules, no valve wings and no closing bodies. Expanding keels are parallel with divergent tips (Figure 6), and are dark brown in *F. pulchra* and lighter brown in *F. humilis*. Covering membranes are reduced to a ledge in both cases.

Seeds

From Figure 7 it can be seen that the seed of *F. pulchra* is quite different from that of *F. humilis*. In *F. pulchra* (Figure 7A) the end where the seed has been

attached to the funicle (hilar end) has a sharp point, whereas in *F. humilis* it is more rounded. The length of the micropylar regions appears to be similar in the two species. The surface sculpturing is irregular in both species of *Frithia* (Figure 7B, E) and although there are no microbaculae present, the surface of the epidermal cells differs markedly between the two species (Figure 7C, F), that of *F. pulchra* being rough-textured whereas the cell surface of *F. humilis* is smoother.

NEAREST RELATIVES

The position of *Frithia* within the *Stomatium* Group proposed by Hartmann (1998) has always been tentative because of the outlier geographical distribution range and unique leaf characters displayed by the genus. Perhaps the most unusual feature is the spirally arranged leaves, a unique character within the subfamily Ruschioideae Schwantes in Ihlenf., Schwantes & Straka (1962) emend. Bittrich & H.E.K.Hartmann. Superficially, plants of *Frithia* resemble the genus *Fenestraria* N.E.Br., also with windowed leaf tips. However, *Fenestraria* occurs in northern Namaqualand and Namibia and no other characters are shared by the two genera.

As stated by Hammer (1998), *Frithia* has characters in common with *Delosperma*, but major differences still separate the two genera. One of the similarities is the leaf epidermis which is covered by opaque idioblasts. Idioblasts of *Delosperma deilanthoides* S.A.Hammer (1998) most closely resemble those of *Frithia* and are also arranged in rows. Capsules in both genera lack covering membranes and closing bodies. Distributions of these two genera overlap. The distribution of *Delosperma deilanthoides* is centred in the Steenkampsberg, Mpumalanga. It has similar habitat requirements (sandy, well-drained soil with a high organic content and porous,

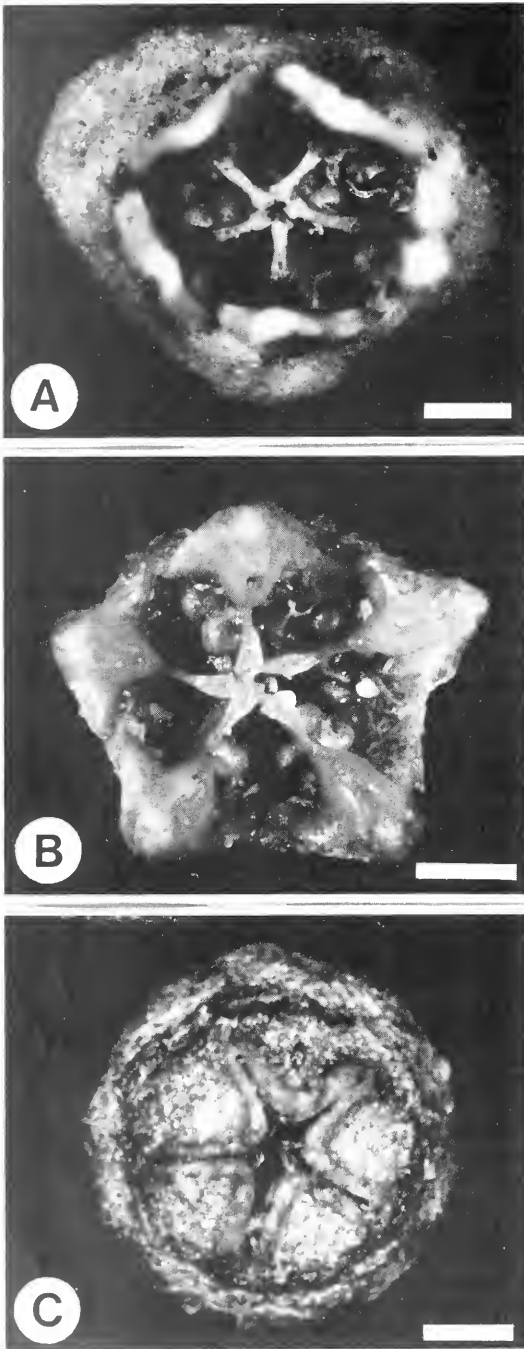


FIGURE 6.—Fruit capsules of *Frithia*: A, *F. pulchra*; B, *F. humilis*; C, closed capsule of *F. humilis*; A, Burgoyne 6699c; B, C, Burgoyne 6694b. Scale bars: 1 mm.

coarse lithology) to those of *Frithia*, but the Steenkampsberg receives a higher rainfall (± 1200 mm per annum). Flowers of both genera belong to the white/pink colour range and open from mid-morning to mid-afternoon (Smith *et al.* 1998). However both flower colour and the presence or absence of epidermal idioblasts are considered to be plesiomorphic and are not suitable to indicate relationships.

The spiral leaf arrangement, not opposite as in other mesembs, gives rise to the interpretation that *Frithia* may have retained this primitive character (spirally arranged leaves are regarded as primitive) while developing advanced states in other characters. A more likely explanation may be that the spiral leaf arrangement found in *Frithia* is a derived feature, since it is not present in any genus holding a more basal position within the Mesembryanthemaceae. Based on this data it could be assumed that *Frithia* may be considered a highly specialised 'Delosperma'.

The leaves of *Neohenricia sibbettii* (L.Bolus) L.Bolus most closely resemble those of *Frithia* (Figure 2C) in shape, but the leaf surfaces of these two genera differ markedly. Leaves of *Neohenricia* are covered by wart-like crustose epidermal outgrowths, with opaque idioblasts scattered among them. Leaves of *Neohenricia* are opposite, whereas those of *Frithia* are arranged spirally. Capsules of the two genera are similar except that those of *Neohenricia* have four to six locules (four locules being the norm) and are shallow; those of *Frithia* are five- or six-locular and barrel-shaped. Moreover, the capsules of *Neohenricia* are borne on a remarkably thin pedicel and stand above the mass of leaves, whereas those of *Frithia* are buried within the leaves on a short pedicel and tend to be expelled via leaf pressure when ripe. However, flower colour and morphology differ considerably. Flowers of *Neohenricia* are pale yellow, borne on long pedicels and have thin spiky petals, opening in the mid-afternoon to evening. Nectaries are in the form of a glandular ring in *Neohenricia*, whereas those of *Frithia* are free. Flowers of both genera have very short stigmas with the staminodes and stamens that are fused, almost forming a hypanthium. The distribution ranges of these two genera do not overlap.

Further investigation is being done to examine the relationship (if any) between *Conophytum limpidum* S.A.Hammer and *Frithia* (Burgoyne in prep.) as they have some characters in common: a hypanthium is present; the petals, petaloid staminodes and anthers are comparable; windowed leaf tips present; fruit capsules can be compared as closing bodies; covering membranes are absent. Both are summer rainfall mesembs.

CONSERVATION STATUS

Use of the IUCN red list of categories (IUCN Species Survival Commission 1994), indicate that both species of *Frithia* should be regarded as Vulnerable, as the total area that they occupy is less than 100 km². Although the areas where these species grow are not in any immediate danger of being destroyed because they are too rocky, the limited distribution poses the risk that human activity could wipe out a large part of the populations should their habitat be used and transformed in the future. One locality of *F. humilis* is situated at the edge of an informal housing development, but the habitat is so unsuitable for any utilisation by man that it has remained largely undisturbed except for littering. The conservation status of *F. pulchra* is more secure, as a large part of the population is situated in the Rustenburg Nature Reserve. All other areas where populations of both species of *Frithia*

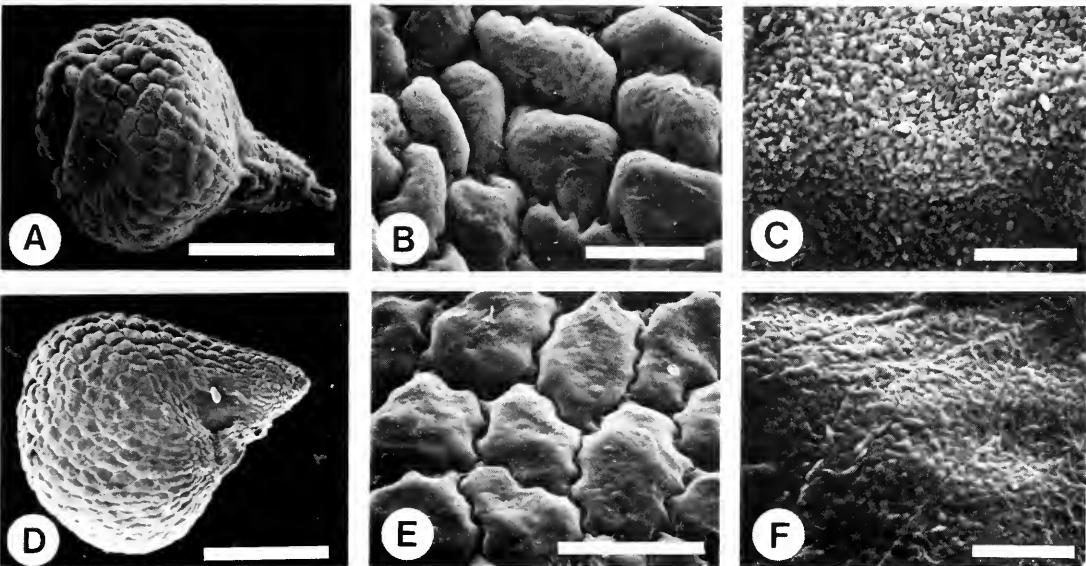


FIGURE 7.—Seed of *Frithia*: SEM micrographs: A–C, *F. pulchra*, Burgoyne 6699c; D–F, *F. humilis*, Burgoyne 6694b. Scale bars: A, D, 100 µm; B, E, 10 µm; C, F, 1 µm.

grow are in the hands of private land owners, many not even aware of the presence of these tiny plants. Unscrupulous succulent collectors may pose the greatest threat to populations of *Frithia*. Further population studies of both species of *Frithia* will be undertaken and their new conservation status will be determined (Burgoyne, Krynanuw & Smith in prep.).

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A review of generic concepts in the Stilbaceae

J.P. ROURKE*

Keywords: *Eurylobium* Hochst., generic review, *Kogelbergia* Rourke, new combinations, new genus, *Retzia* Thunb., Stilbaceae

ABSTRACT

The generic concepts in the Cape endemic family Stilbaceae (± 14 species), are reviewed. Proposals by various authors to include *Retzia capensis* Thunb. in the Stilbaceae are supported. *Xeroplana* Briq. and *Eurylobium* Hochst. are shown to be congeneric with *Stilbe* L., resulting in one new combination and one new name in *Stilbe*. Seven currently recognised species of *Stilbe* are enumerated. A key to the genera of the Stilbaceae, as presently understood, is provided. A new genus *Kogelbergia* is described to accommodate two species previously assigned to *Stilbe* sect. *Amphistilbe* and two new combinations in *Kogelbergia* are proposed.

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INTRODUCTION

The Stilbaceae Kunth, a small family in the Lamiales, is endemic to the southern Western Cape. It is variously regarded as a subfamily within the Verbenaceae by some authors (Cronquist 1981) or as a family by others (Dyer 1975; Dahlgren 1980). The entire family consists of about twelve currently recognised species arranged in six genera.

Four of these (*Eurylobium* Hochst., *Campylostachys* Kunth, *Euthystachys* A.DC. and *Thesmophora* Rourke) are monotypic. While *Campylostachys* and *Thesmophora* are defined on sound morphological characters, *Eurylobium* and *Xeroplana* Briq. (two species) are here considered to be congeneric with *Stilbe* L. On present evidence *Euthystachys* seems sufficiently distinct to be upheld as a monotypic genus but further studies of fresh material from a range of populations are required before an adequate assessment can be made. Over and above these genera there is material of at least one and possibly two further undescribed taxa represented in local herbaria so it is unlikely that the final species count for the family will exceed fourteen.

INCLUSION OF *RETZIA* IN THE STILBACEAE

Before discussing these generic concepts any further, the position of *Retzia* Thunb. must also be considered in any review of the Stilbaceae and its relationships.

Retzia capensis Thunb., a monospecific endemic Cape genus, has been assigned to a wide range of families since it was described by Thunberg in 1776 (see Dahlgren *et al.* 1979, for a detailed review of its past taxonomic history). It has also been treated as a monospecific family (Dyer 1975). Similarly, Cronquist (1981) upheld the Retziaceae as a monospecific family, dismissing any relationship with the Stilbaceae largely on account of the placentation and 'organisation of the gynoeceum' in *Retzia*. In a similar view, Takhtajan (1997), while acknowledging that Stilbaceae and Retziaceae are closely related, continued to uphold both as separate families. However, modern data from several different sources now indicate conclusively that *Retzia* is most closely allied to the Stilbaceae.

In a comparative study of iridoid glucosides in *Stilbe ericoides* L. and *Retzia capensis*, biogenetically similar compounds were found in both species (Dahlgren *et al.* 1979). These authors further pointed out that morphological and anatomical evidence also suggested a close relationship between the two families. An extensive investigation of the wood anatomy of several genera in the Stilbaceae has further highlighted the similarities between *Retzia* and the Stilbaceae (Carlquist 1986). More recently, *rbcL* sequences for *Euthystachys* (Stilbaceae) and *Retzia* were found to be very similar, 'differing by only eight substitutions', (Bremer *et al.* 1994), again confirming the close relationship between the two families. Thus morphological, anatomical, phytochemical and molecular evidence supports the inclusion of *Retzia* in the Stilbaceae.

In an updated phylogenetic classification of the flowering plants, Thorne (1992) incorporated *Retzia* into the Stilbaceae, dividing the Stilbaceae in two subfamilies, Retzioideae and Stilboideae. This view is followed in the present treatment and is, similarly, the current opinion of the Angiosperm Phylogeny Group (1998).

STILBACEAE SUBFAMILY STILBOIDEAE

All members of the the Stilbaceae subfamily Stilboideae are small, inconspicuous ericoid shrublets with very small white or pinkish flowers. Although typical components of the Cape fynbos they are never dominant

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and tend to be easily overlooked. Several taxa are rare localised endemics, and some are possibly palaeoendemics. In almost all cases the flowers are extremely small (shorter than 10 mm) which has made the dissecting and interpretation of herbarium material very difficult, often leading to serious misinterpretations of the floral structures (Rourke 1977). During the course of revising the family I have been able to examine a wide range of fresh living material collected in the field which has greatly clarified an understanding of the floral structures.

This review of the generic characters within the family has led to an expanded concept of *Stilbe* which will be discussed here and also the exclusion from *Stilbe* of two species previously known as *Stilbe mucronata* N.E.Br. [more recently as *Stilbe verticillata* (Eckl. & Zeyh.) Moldenke] and *Stilbe phyllicoides* A.DC. It is proposed that they be placed in a new genus, *Kogelbergia* Rourke.

As presently understood the Stilbaceae subfamily Stilboideae consists of five genera, two of which are characterised by having four-lobed corollas (*Campylostachys* and *Thesmophora*) and three which have five-lobed corollas (*Stilbe*, *Euthystachys* and *Kogelbergia*).

CURRENT GENERIC POSITION

The problem of finding a rational generic classification of the Stilbaceae has been known for some time (Dyer 1975; Rourke 1977). In this review an interim solution is provided to satisfy the immediate needs of two generic treatments of the family for 'Seed plants of southern Africa: families and genera' and K. Kubitski's 'The families and genera of vascular plants', currently in progress. A major taxonomic difficulty concerns the present circumscription of *Stilbe*, *Xeroplana*, *Eurylobium* and *Euthystachys*.

Stilbe L.

Two distinct groups can be recognised within *Stilbe* based on the symmetry of the corolla and the presence or absence of pubescence on the corolla lobes.

Stilbe verticillata and *S. phyllicoides* A.DC. have actinomorphic corollas and densely pubescent corolla lobes of equal size [*Stilbe* sect. *Amphistilbe* (Pearson 1901)]. The ovary in both species is single-chambered (but has marginal septum remnants), with two basal ovules.

The remaining species are characterised by prominently bilabiate flowers with two broad, erect posterior corolla lobes and three narrow anteriorly deflected corolla lobes, all of which are quite glabrous [*Stilbe* sect. *Eustilbe* (Pearson 1901)]. The sepals are fused to form a tubular, usually glabrous calyx. The ovary is two-chambered with a single ovule in each chamber. At anthesis one of the ovules and its locule aborts, leaving a single ovule in a single chamber.

It is proposed that the present broad circumscription of *Stilbe* be emended to encompass merely *Stilbe* sect. *Eustilbe* and that the two species currently placed in

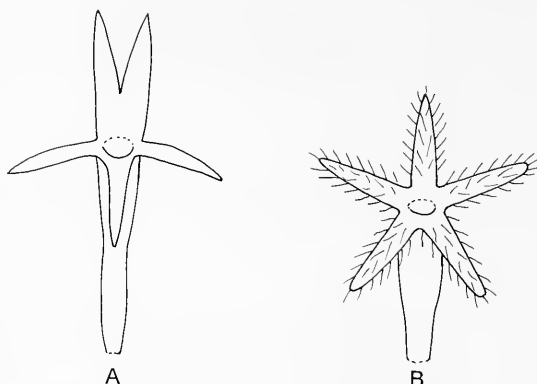


FIGURE 1.—Diagrammatic representation of the differences in corolla structure and pubescence between A, *Stilbe* and B, *Kogelbergia*.

Stilbe sect. *Amphistilbe* be removed to a new genus, herein described as *Kogelbergia* (Figure 1).

Xeroplana Briq.

In *Xeroplana* the corolla is strongly bilabiate with two broad, erect posterior petals, and three narrow anterior petals. The corolla lobes are glabrous. Initially the ovary is two-chambered with a single ovule in each chamber, but the abaxial chamber and ovule soon abort, leaving a single adaxial chamber with a solitary basal ovule. These similarities with *Stilbe* sect. *Eustilbe* have already been noted; moreover, it has previously been pointed out that the generic status of *Xeroplana* is questionable (Rourke 1977). On the basis of gross morphological evidence *Xeroplana* and *Stilbe* sect. *Eustilbe* are congeneric. Consequently, as no rational justification can be found to uphold *Xeroplana*, it is proposed that it be merged with *Stilbe* sect. *Eustilbe* under a modified concept of *Stilbe*, after having removed the two species in *Stilbe* sect. *Amphistilbe* to a new genus, *Kogelbergia*.

Eurylobium Hochst.

Vegetative and floral characters in *Eurylobium* are the same as in *Stilbe* sect. *Eustilbe*, namely, a tubular corolla, strongly bilabiate with two large, erect posterior lobes and three narrower, anteriorly deflected lobes. The corolla lobes are glabrous. The sepals are fused for $\frac{3}{4}$ of their length to form a glabrous, actinomorphic calyx tube. Initially the ovary is bilocular with an ovule in each chamber but at an early stage one of the ovules aborts, leaving the ovary to become unilocular with a single, functional, basally attached ovule. As these characters are the same as in *Stilbe* sect. *Eustilbe*, there is no justification for upholding *Eurylobium* as a monotypic genus.

Euthystachys A.DC.

The single species in this monotypic genus, *E. abbreviata* A.DC. is distinguished by the following characters: soft, pubescent sepals fused for about $\frac{1}{4}$ of their length at the base; an actinomorphic corolla of five, glabrous, equal corolla lobes and a bilocular ovary with a single functional ovule in each chamber.

These characters, though slender, provide sufficient justification for maintaining *Euthystachys* as a monotypic genus at this stage. Nevertheless, there are some differences in the degree of fusion of the sepals in certain collections. Further field work and the study of a range of fresh material is required before the generic status of *Euthystachys* can be adequately assessed.

Under the revised generic concept of *Stilbe* discussed above, two genera in the family, *Xeroplana* Briq. and *Eurylobium* Hochst. fall clearly within the emended circumscription of *Stilbe* and must be reduced to synonymy as indicated below.

SYNOPSIS OF *STILBE*

Stilbe P.J.Bergius, Descriptiones plantarum ex Capite Bonae Spei: 30, t. 4 (1767); H.Pearson: 183 (1901). Type: *Stilbe vestita* P.J.Bergius.

Eurylobium Hochst.: 228 (1842); Walp.: 173 (1845); A.D.C.: 608 (1848); H.Pearson: 187 (1901). Type: *Eurylobium serrulatum* Hochst.

Xeroplana Briq.: 336 (1896); H.Pearson: 188 (1901); Rourke: 1 (1977). Type: *Xeroplana zeyheri* Briq.

Ericoid shrublets, 0.5–1.5 m tall, with a single main stem, occasionally multistemmed and lignotuberous. Leaves ericoid, linear-subulate to narrowly lanceolate, ascending, in whorls of 3–5, margins revolute. Inflorescence a dense sessile spike, 10–40 mm long. Flowers white or pink, sessile, subtended by single anterior bract. Floral bracts 2, opposite, foliaceous. Calyx tubular, usually hard, with 5 free lobes occasionally slightly abaxially curved. Corolla tubular, 5-merous, bilabiate with two erect glabrous posterior lobes and three narrower glabrous anterior lobes; interior of throat ringed with dense pubescence, only rarely glabrous. Stamens 4, equal, posterior stamen absent; filaments glabrous, filiform; anthers basifixed. Ovary oblong, laterally compressed, potentially two-chambered but abaxial chamber abortive; adaxial chamber with a single basally attached ovule; style filiform glabrous, slightly adaxially curved; apex occasionally minutely bilobed. Fruit cylindric, laterally compressed, brown, shiny, dehiscing into 2 valves at apex. Seeds ovoid, straw-coloured.

An enumeration of the species of *Stilbe* currently recognised within the new delimitation of the genus is given here.

1. *Stilbe vestita* P.J.Bergius, Descriptiones plantarum ex Capite Bonae Spei: 30, t. 4 fig. 6 (1767).

2. *Stilbe ericoides* L., Mantissa plantarum altera: 305 (1771).

3. *Stilbe albiflora* E.Mey., Commentariorum de plantis Africae australioris 1: 279 (1836).

4. *Stilbe rupestris* Compton in Journal of South African Botany 10: 127, 128 (1944).

5. *Stilbe serrulata* (Hochst.) Rourke, comb. nov.

Eurylobium serrulatum Hochst. in Flora 15: 229 (1842). Type: 'Inter rupes cacuminis montis prope Genadenthal in Colonia Capensis' Dec. 1838, Krauss 1110, TUB6019 (TUB, holo.).

6. *Stilbe overbergensis* Rourke, nom. nov.

Xeroplana zeyheri Briq. in Bulletin de l'Herbier Boissier, Sér. 1, 4: 336 (1896). Type: Western Cape, on banks of Riviersonderend River at Appelskraal and on adjacent mountains Ecklon & Zeyher sub *Stilbe* sp. nov. no. 8 in herb. Delessert (G, holo.).

The epithet *zeyheri* cannot be used due to the prior existence of *Stilbe zeyheri* Gand. (1913), a synonym of *Stilbe albiflora* E.Mey.

7. *Stilbe gymnopharyngia* (Rourke) Rourke, comb. nov.

Xeroplana gymnopharyngia Rourke in Journal of South African Botany 43: 6 (1977). Type: Western Cape, Langeberg Mountains, Riversdale above the Farm Langkloof on 'Annex Langekloof', along summit ridge. Rourke 1451 (NBG, holo., PRE, BOL, K, MO, G, S, iso.).

Key to genera of Stilbaceae

- 1a Corolla tube 45–55 mm long, pubescent externally, orange-red with black tips (subfamily Retziaceae) *Retzia*
- 1b Corolla tube shorter than 12 mm, glabrous externally, uniformly mauve, pink or white (subfamily Stilboideae):
 - 2a Corolla 4-lobed:
 - 3a Sepals free; corolla lobes glabrous *Campylostachys*
 - 3b Sepals fused forming tube; corolla lobes pubescent *Thesmophora*
 - 2b Corolla 5-lobed:
 - 4a Corolla actinomorphic; lobes equal or almost equal:
 - 5a Corolla lobes pubescent *Kogelbergia*
 - 5b Corolla lobes glabrous *Euthystachys*
 - 4b Corolla prominently bilabiate with two larger erect posterior petals and three narrow anterior petals *Stilbe*

KOGELBERGIA, A NEW GENUS IN THE STILBACEAE

As previously mentioned, it is proposed that the two species in *Stilbe* sect. *Amphistilbe* be removed to a new genus, *Kogelbergia*. Its distinguishing characters are discussed here.

Inflorescence structure

Superficially the inflorescence appears to be a sessile, globose capitulum. However, careful dissection of *K. verticillata* indicates that it is paniculate in structure with several highly condensed axillary branches bearing 3 or 4 flowers. The inflorescence structure in all other Stilbaceae subfamily Stilboideae is spicate. It seems probable that although much reduced and condensed, the paniculate inflorescence of *K. verticillata* represents a less specialised condition than the racemose pattern in the rest of the Stilbaceae. In *K. phyllicoides* the inflorescence is a condensed spike with no trace of a paniculate structure.

Corolla

Although the corolla is actinomorphic at anthesis consisting of 5 equal, linear corolla lobes, as the corolla opens, two lobes briefly assume an erect (posterior) position with the remaining three assuming a patent (anterior) position. This condition can only be briefly detected by observing developmental stages in living material and

is soon lost as the flower matures. It seems probable that actinomorphy in the corolla is a plesiomorphic condition with bilateral symmetry and a bilabiate corolla representing the derived condition.

The presence of dense villous pubescence on the linear corolla lobes of *Kogelbergia* is a character highly unusual in the family. All other Stilbaceae except *Thesmothora* and *Retzia*, have completely glabrous corolla lobes. This pubescence is formed by the presence of 1–2 mm long white trichomes on the inner surface, apex, and outer surface of each corolla lobe. Like almost all other Stilbaceae, *Kogelbergia* has a distinctive ring of pubescence in the throat of the corolla. Only three other species in the entire family lack this feature. The dense pubescence on the apices of the corolla lobes appears to be unrelated to the throat pubescence and is regarded here as a completely new character.

Ovary

Typically the ovary in Stilbaceae subfamily Stilboideae is bilocular with a single ovule in each chamber, or initially bilocular but with one abortive ovule in an atrophied or abortive second locule leaving a single functional ovule to develop. In *Kogelbergia* the ovary is unilocular with two basal ovules. However, serial sectioning of the ovary shows clear remnants of a septum in the position where this would normally be expected to be (i.e. at right angles to the axis). The septum breaks down very early in the development of the ovary leaving a unilocular condition which is clearly derived (Figure 2).

Pollen

A review of pollen structure in the Stilbaceae (excluding *Retzia*) showed that the pollen of the ‘*Stilbe mucronata* type’ was quite distinct within the family (Raj

TABLE 1.—Summary of major morphological differences between *Stilbe* and *Kogelbergia*

<i>Kogelbergia</i>	<i>Stilbe</i>
Corolla actinomorphic at anthesis, of 5 equal petals	Corolla strongly zygomorphic, bilabiate with 2 erect posterior petals and 3 patent anterior petal limbs. Corolla lobes not equal
Corolla lobes densely pubescent	Corolla lobes glabrous
Inflorescence a condensed globose panicle or spike	Inflorescence a spike
Ovary single-chambered with two basal ovules	Ovary two-chambered with a single ovule in each chamber, one ovule/chamber often aborting
Pollen exine striato-reticulate (Raj 1983)	Pollen exine rugulose, tectate (Raj 1983)

1983). Instead of having a rugulose exine (as in *Campylostachys*) or tectate-perforate exine as in the remaining species in the family, the exine of *Kogelbergia* (the ‘*Stilbe mucronata* type’) has a striato-reticulate exine, setting it apart from all its congeners (Raj 1983).

Conclusion

Fundamental morphological differences exist between the two species previously known as *Stilbe verticillata* and *Stilbe phyllicoides* and other members of the genus *Stilbe* (Table 1). These are considered sufficient to justify separate generic status. Accordingly, a new genus *Kogelbergia* is described to accommodate these species. Part of the distribution area of one of these species falls within the Kogelberg Nature Reserve, one of the centres of the highest endemism in the Cape Floristic Kingdom.

***Kogelbergia* Rourke**, genus novum *Stilbei* affine, a quo corolla actinomorpha 5 petalis aequalibus lobis dense pubescentibus, et ovario uniloculari ovulis duobus basilaribus, differt. Typus: *Kogelbergia verticillata* (Eckl. & Zeyh.) Rourke.

The genus *Kogelbergia* is distinguished from all other genera by its dense, globose, sometimes inconspicuously branched (apparently paniculate) or spicate inflorescences, the actinomorphic corolla, 5 equal petals densely pubescent at their apices, and the single-chambered ovary with 2 basal ovules. Two species are currently recognised.

***Kogelbergia verticillata* (Eckl. & Zeyh.) Rourke**, comb. nov.

Trichocephalus verticillatus Eckl. & Zeyh., Enumeratio plantarum africae australis 131 (1835). *Stilbe verticillata* (Eckl. & Zeyh.) Moldenke: 474 (1948). Type: in lateralibus montium prope Palmietrivier, supra Grietjiesgat, June, Alt. 4, Ecklon & Zeyher 1003 (SAM, iso.!).

Stilbe mucronata N.E.Br.: t. 2526 (1897); H.Pearson: 184 (1901). Type: in declivibus montium Houwhoeck, April 1895, 1400 ped., *Bolus* 8409 (K, lecto.! here designated).

Stilbe mucronata N.E.Br. var. *cuspidata* H.Pearson: 184 (1901). *S. verticillata* (Eckl. & Zeyh.) Moldenke var. *cuspidata* (H.Pearson)

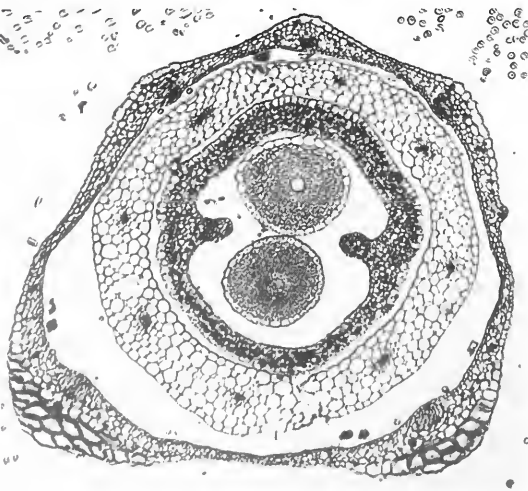


FIGURE 2.—*Kogelbergia verticillata*; cross section through base of ovary showing single chambered ovary with two ovules, $\times 77$. Note remnant of ovary septum placed at right angles to inflorescence axis. Two anterior sepals at base of calyx tube slightly larger than posterior sepals.

Moldenke: 474 (1948). Type: Zwartberg, Caledon, Dec., *Bolus s.n.* (K, holo.).

Stilbe chorispala Suess.: 56 (1950). Type: Franschoek Pass, 17-11-1946, S. Rehm in herb. W. Giess 1377 (M, holo.).

Small, rigid, well-branched shrublet up to 1 m high with a single main trunk up to 50 mm diam. *Flowering branches* 2–3 mm diam., densely lanate initially, later becoming glabrous. *Leaves* in whorls of 5, patent to slightly recurved, ericoid, narrowly lanceolate, 10–12 × 2 mm, apices prominently mucronate, upper surface glabrous when mature, under surface lanate, margins recurved. *Inflorescence* a sessile, globose, much condensed panicle 15–22 mm diam; lateral axes much condensed, bearing 3 or 4 flowers; each flower subtended by a lanceolate-acute, apically mucronate bract and two opposite floral bracts. *Floral bracts* very narrowly oblanceolate, glabrous basally but lanately crinite apically. *Calyx* actinomorphic, tubular, 5 mm long, of 5 equal lobes (but anterior sepals slightly thicker at base), fused into a glabrous tube for $\frac{1}{4}$ of their length; free lobes very narrowly oblanceolate, glabrous basally but lanately crinite apically. *Corolla* 8–10 mm long, funnel-form, tubular, tube region glabrous, hyaline, actinomorphic but the 2 posterior petals erect, three anterior petals patent at anthesis; throat fringed with a dense ring of lanate pubescence; lobes at anthesis linear-acuminate, densely tomentose. *Stamens* 4, prominently exserted, 5 mm long, inserted between corolla lobes; posterior stamen absent; anthers versatile, dorsifixed, sagittate. *Ovary* ellipsoid, purple in upper half, bilaterally flattened, single-chambered with 2 basal ovules in chamber; style straight, terete, 6–7 mm long. *Seed* cylindrical-ovoid, 2 mm long, surface colliculate, tending to tuberculate basally, pale straw-coloured (Figure 3).

Distribution, habitat and biology

This species ranges in an arc from French Hoek Pass southwards through the Hottentots Holland Mountains to Kogelberg; thence eastwards to the Caledon Swartberg and Genadendal in the Rivieronderend range. Outlying populations occur in the mountains near Napier and Elim with an isolated collection made on the Potteberg. *Kogelbergia* is essentially a montane species occurring mainly above 450 m, but may range from 250–1 150 m. It generally favours moist south-facing habitats and is often found in peaty soil overlying Table Mountain Sandstone. *Flowering time*: May–November. Seeds are shed in January (Figure 4).

Specimens examined

WESTERN CAPE.—3318 (Cape Town): Jonkershoek, east of top of zig-zag path above 2nd waterfall, (–DD), Jan., *Rycroft* 146 (PRE). 3319 (Worcester): Franschoek Pass, (–CC), Nov., *Rehm* in herb. W. Giess 1377 (M). 3418 (Simonstown): east of Kogelberg at summit of peak at north end of Five Beacon Ridge, (–BB), June, *Rourke* 479 (NBG, PRE); mountains of Sir Lowry's Pass, March, *Burchell* 8821 (K, PRE); southeast slopes of Moordenaarskop, (–BD), July, *Boucher* 3056, April, *Boucher* 1242 (NBG). 3419 (Caledon): Dwaarsberg, Hottentots Holland Mountains, (–AA), Jan., *Rourke* 1844 (NBG, PRE); Kathleen Murray Nature Reserve, Nuweberg Forest Reserve, June, *Rourke* 1968 (NBG); top of ridge east of Viljoen's Pass, June, *Goldblatt* 2049 (NBG); Houwhoek, April, *Schlechter* 7574 (K, PRE, SAM); in lateralibus montium prope Palmietrivier supra Grietjiesgat, June, *Ecklon* &

Zeyher 1003 (SAM); Hottentots Holland Mts, July, *Ecklon* & *Zeyher* 2215 (SAM); Lebanon Catchment, Grabouw, June, *Kruger* 76 (PRE); Swartberg, Caledon, (–AB), Oct., *Bodkin* in herb *Bolus* 6785 (NBG, PRE); *Bolus s.n.* (K); Highlands, (–AC), Aug., *Compton* 7348 (NBG); Genadendal, (–BA), Dec., *Bodkin* in herb. *Guthrie* 3623 (NBG); Boskloof Farm, eastern ridges of Paardeberg, (–BC), Dec., *Rourke* 2053 (NBG); Groot Hagel Kraal, Haelkraal River area, NE of farmstead, (–DA), April, *Oliver* 5884 (NBG); Elim, (–DB), April, *Schlechter* 7636 (K, PRE, NBG). 3420 (Bredasdorp): Potteberg, Albertsdal Farm, (–BC), May, *Compton* 19526 (NBG).

Kogelbergia phylicoides (A.DC.) Rourke, comb. nov.

Stilbe phylicoides A.DC., Prodrum systematis naturalis regni vegetabilis 12: 606 (1848); H.Pearson: 183 (1901). Type: Voormansbosch near Swellendam (sub loc. no. 70), *Zeyher* 3589 in herb. Boiss. (G, holo.; K!, SAM!).

Campylostachys phylicoides Sond.: 202 (1847), nom. nud.

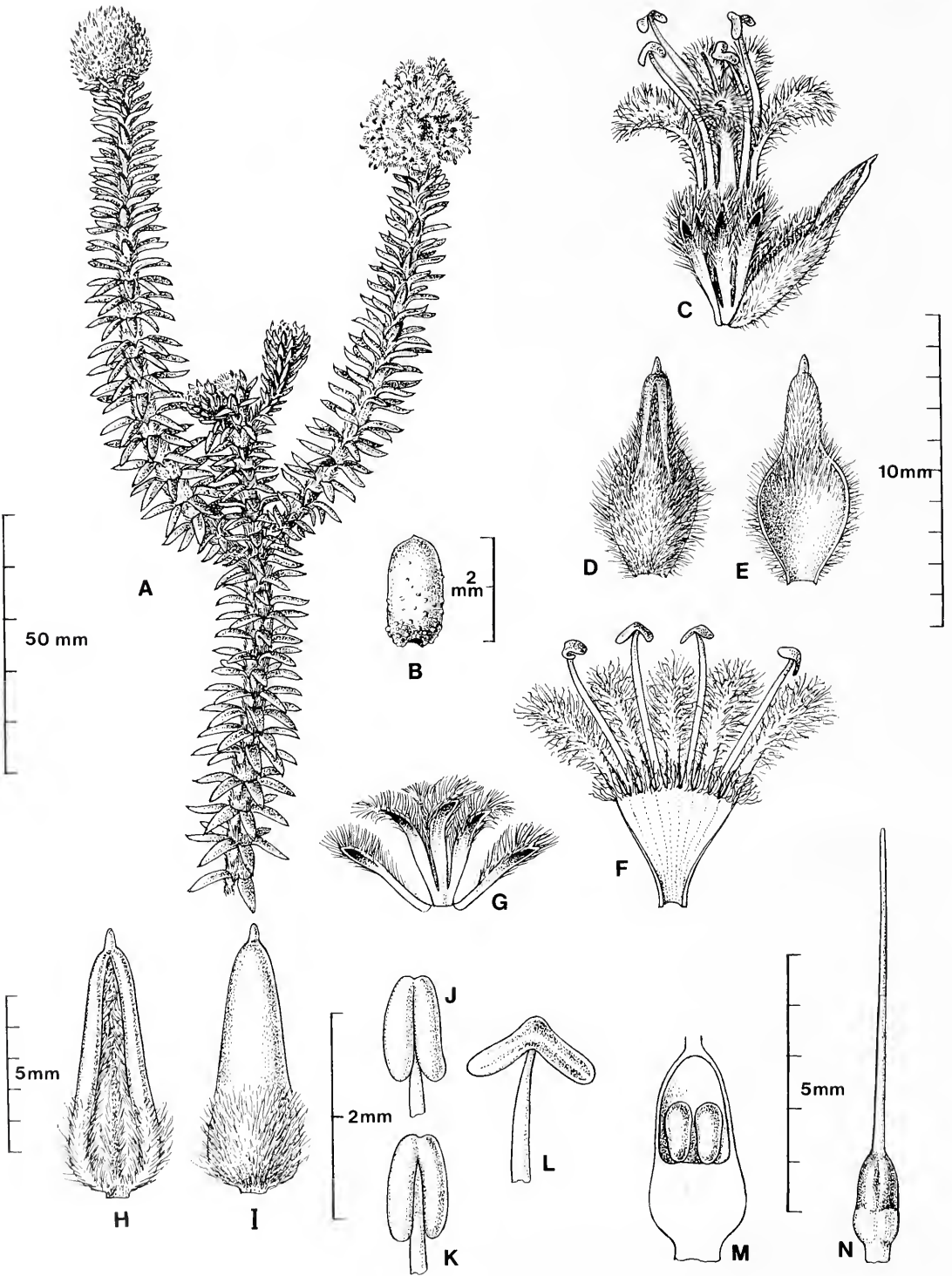
Small, upright, multiple-stemmed, lignotuberous shrublet, 0.5–1.0 m tall. *Flowering branches* sparsely sericeous initially, soon glabrous, 1–3 mm diam.; lower branches covered in prominent leaf scars. *Leaves* in pseudowhorls of 5–7, patent to slightly incurved, ericoid, very narrowly lanceolate-linear, 5–12 × 1 mm, glabrous, apices curved upwards, strongly mucronate. *Inflorescence* a sessile, globose to ovoid terminal spike, 20–25 × 15 mm, usually solitary, occasionally with up to 3 axillary spikes clustered below; each flower subtended by a lanceolate-cymbiform bract, sericeous proximally, apex glabrous, mucronate. *Floral bracts* 2, narrowly lanceolate-acuminate, 5–7 × 1 mm, sparsely sericeous, hyaline. *Flowers* sessile. *Calyx* with 5 sepals; sepals free, narrowly lanceolate, 6–7 × 1 mm, hyaline to papyraceous, upper half sericeous, apices prominently rostrate; posterior sepal smaller than remainder. *Corolla* actinomorphic, 8–10 mm long; lobes narrowly lanceolate-acuminate, patent, densely pubescent mainly on inner surface, 2–3 mm long; tube glabrous 4–5 mm long; throat fringed with dense ring of pubescence. *Stamens* 4, exserted, 5–6 mm long, inserted between corolla lobes; posterior stamen absent; anthers versatile, dorsifixed, sagittate. *Ovary* 1 mm long, ovoid, bilaterally flattened, single-chambered with two basal, erect ovules; style straight, terete, 6 mm long. *Seeds* not seen.

Distribution, habitat and biology

Endemic to the Langeberg Range in the southern Western Cape, *Kogelbergia phylicoides* occurs sporadically on the upper south slopes in mesic mountain fynbos between the Clock Peaks at Swellendam and the Robinson Pass near Mossel Bay (Figure 4). Populations are mostly small, usually consisting of less than 12 individuals, and are generally found at elevations between 425 and 1 100 m. *Flowering time*: October and November.

Specimens examined

WESTERN CAPE.—3320 (Montagu): first path below 10 O'clock Peak, Swellendam, (–CD), Oct., *Wuris* 445 (NBG); Langeberg, Swellendam, south slope of 12 O'clock Peak, Oct., *Taylor* 7203 (NBG, K); Voormansbosch, (–DC), Oct., *Zeyher* 3589 (K, SAM); Zuurbraak Peak, Oct., *Barnard* SAM37286 (SAM). 3321 (Ladismith): Garcia's Pass, Riversdale, (–CC), Oct., *Thorne* SAM38850; Garcia's Pass, Oct.,



EWVH 1992

FIGURE 3.—*Kogelbergia verticillata*, Rourke 1968. A, flowering shoot; B, mature seed; C, open flower and subtending bract; D, bract, abaxial view; E, bract, adaxial view; F, corolla, opened; G, calyx and two floral bracts; H, leaf, adaxial view; I, leaf, abaxial view; J, K, anthers before dehiscence; L, anther after dehiscence; M, longitudinal section through ovary; N, gynoecium. Scale bars: A, 50 mm; B, J–L, 2 mm; C–G, 10 mm; H, I, M, N, 5 mm.

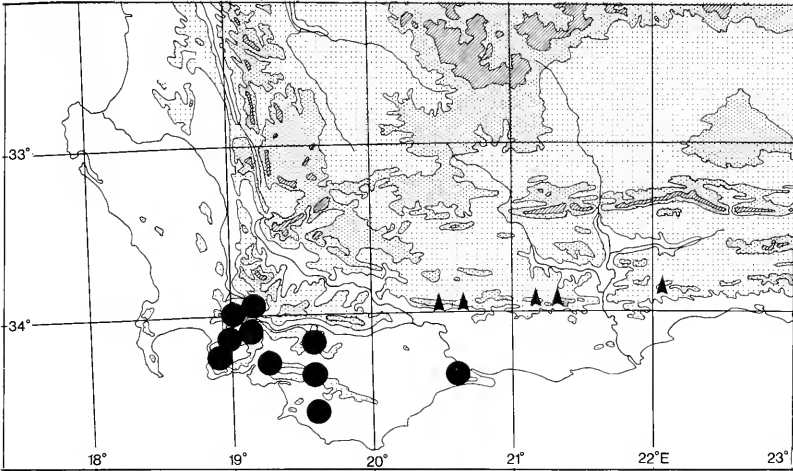


FIGURE 4.—Distribution of *Kogelbergia verticillata*, ●, and *Kogelbergia phyticoides*, ▲.

Galpin 4420 (K, PRE); summit of Kampscheberg, Riversdale, 9-12-1814, *Burchell 7127* (K, PRE); lower part of Kampscheberg, 1-12-1814, *Burchell 6937* (K); Langeberg Mountains, Riversdale, above Farm Langkloof on 'Annex Langekloof', Nov., *Rourke 1446* (NBG). 3322 (Oudtshoorn): Robinson's Pass, Outeniqua's, (-CC), Oct., *Bond 1567* (NBG).

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Studies in the Sphaerocarpaceae (Hepaticae) from southern Africa. 2. The genus *Sphaerocarpos* and its only local species, *S. stipitatus*

S.M. PEROLD*

Keywords: *Austrosphaerocarpos* (subgenus), Hepaticae, Monocarpineae, Riellineae, southern Africa, Sphaerocarpaceae, Sphaerocarpaceae, Sphaerocarpaceae, *Sphaerocarpos stipitatus*

ABSTRACT

A taxonomic account of the genus *Sphaerocarpos*, subgenus *Austrosphaerocarpos*, and its only local species, *S. stipitatus* Bisch. ex Lindenb., is presented here. These taxa are classified in the suborder Sphaerocarpineae of the order Sphaerocarpaceae, for which short notes and a key to all three constituent suborders, Monocarpineae, Riellineae and Sphaerocarpineae, are provided.

INTRODUCTION

The genus *Sphaerocarpos* (Micheli) Boehmer was first recorded from southern Africa by Proskauer (1954). He received material from the algologist, Dr M.A. Pocock, who had collected it in the Eastern Cape, on the banks of pools in the Palmiet River, a tributary of the New Years River, seven miles from Grahamstown, on the Cradock Road. Miss Lilian Britten, a lecturer at Rhodes University College, had originally discovered *Sphaerocarpos* plants at this locality. A further collection from Clanwilliam, by Prof. E.A.C.L.E. Schelpe, was also recorded by Proskauer.

Arnell (1963) did not report any new collections and the only recent published South African record of the species is by Long (1993) from a 1969 collection, *H.R. Toelken 1978* (BM, BOL) from Paardeneiland, Cape Town.

Seven of the collections that I studied, have not been reported in the literature before. Despite repeated visits to the Northern, Western and Eastern Cape by various collectors, myself included, such a small number of gatherings must surely reflect the rarity of these plants, although Proskauer (1955) remarked that, 'one does not normally find members of the group in the field without being familiar with them'. Their truncated life cycle, from spore to spore, can take less than 45 days (Schuster 1992), and dramatically reduces the time period during which they are likely to be found.

It is, nonetheless, hoped that the present, fully illustrated paper, will familiarise more botanists with these remarkable plants and that, in future, they will collect them, thus enabling us to establish the local distribution range more completely. Previously, it was thought that *S. stipitatus* was restricted to the southern hemisphere, i.e. Chile in South America (where the type specimen had been collected by Bertero in 1829) and South Africa. Recently, however, it was also collected as a presumed adventive in Portugal (Sérgio & Sim-Sim 1989), as well as at a remote, high altitude locality in East Nepal (Long 1993), where its accidental introduction is unlikely.

This paper on *Sphaerocarpos stipitatus*, is the second in a series of three on the Sphaerocarpaceae in southern Africa.

MATERIAL AND METHODS

The same procedures as outlined in Perold (1999b) were employed in the preparation of the material for examination and photography by compound light microscope and scanning electron microscope.

Order **Sphaerocarpaceae** Covers in New Phytologist 9: 81 (1910); Grolle: 55 (1983); Scott: 63 (1985).

[excluding the American *Geothallus* Campbell and the Mesozoic fossil, *Naiadita* Brodie]

Plants ephemeral, very diverse, terrestrial; sometimes minute, subspherical and pouch-like, occasionally with branched ventral sprouts (Monocarpineae), or somewhat larger, with prostrate, median stems, up to 4 (or more) cell layers thick, pseudodichotomously branching, with wings 2-ranked, lateral, incised, leafy, unistratose (Sphaerocarpineae); otherwise aquatic, semifrondose, stems \pm erect, apical dominance seemingly persistent, with broad, undulating wing on dorsal side, small leaf scales at both sides and ventrally (Riellineae). *Air chambers* and *air pores* (the latter in the carpocephalum wall) present only in Monocarpineae. *Cells* all thin-walled, large, delicate; smaller oil cells found only in Riellineae. *Rhizoids* all smooth.

Asexual reproduction by gemmae, only in Riellineae.

Monoicous in Monocarpineae and rarely in *Riella* species, otherwise dioicous, mostly heterothallic, with male plants much or somewhat smaller. *Antheridia* ovoid to globose, in Monocarpineae located inside air chambers, pedicel long, uniseriate; in Sphaerocarpineae individually surrounded by involucre, crowded together on dorsal surface of stems; in Riellineae enclosed in pockets along margin of undulating wing, pedicel short, uniseriate. *Archegonia* with 6 rows of neck cells, in Monocarpineae borne on archegoniophores, otherwise individually surrounded by large, flask-shaped or pyriform involucre, dorsally on, or along stems of female plants. *Stalk* variable in length, without rhi-

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zoid furrow. *Capsule* globose, cleistocarpous, wall unistratose, cell walls delicate, in Monocarpineae only with small, nodular to elongated thickenings, in other suborders thickenings absent. *Seta* very short, becoming necrotic. *Spores* medium-sized to very large, 40–140 µm diam., sin-

gle in Monocarpineae and Riellineae, mostly remaining in tetrads in Sphaerocarpineae. *Elaters* absent. *Nutritive cells* present in Sphaerocarpineae and Riellineae. Spore release in all three suborders by dissolution or decay of capsule wall and surrounding tissue.

Key to local suborders of Sphaerocarpaceae

- 1a Plants terrestrial; distribution confined to winter rainfall regions of southern Africa; highly diverse in appearance—subspherical and pouch-like or dorsiventrally flattened with lateral, leaf-like lobes; cells uniform, all lacking oil bodies; spores single or in tetrads:
 - 2a Thalli monoicous, very small, subspherical and pouch-like; outer protective layers with air chambers surrounding carpocephalum, the wall in the latter interrupted by barrel air pores; spores single, hemispherical, ornamentation finely tuberculate suborder **Monocarpineae** sensu Carr
 - 2b Plants dioicous, heterothallic, males very much smaller than females, stems dorsiventrally flattened, laterally divided into unistratose, leaf-like lobes, without air chambers and air pores; gametangia surrounded by small or large (depending on sex) flask-shaped involucre; spores in local species remaining in tetrads, ornamentation ridged suborder **Sphaerocarpineae** Cavers
- 1b Plants aquatic; distribution in both winter and summer rainfall regions of southern Africa; uniform in appearance, consisting of erect stem, dorsally bearing undulate wing and small leaf scales at sides and ventrally; cells dimorphic, some with an oil body; spores single, ornamentation various suborder **Riellineae** R.M.Schust.

Sphaerocarpineae Cavers. R.M.Schust.: 807 (1992).

Plants terrestrial, dorsiventrally flattened, bilateral, consisting of a stem (or axis), once or twice to repeatedly furcate, laterally invested with delicate, leaf-like lobes. *Ventral* scales absent, instead invested with ephemeral slime papillae. *Cells* thin-walled, lacking oil bodies. *Rhizoids* all smooth, hyaline.

Asexual reproduction absent.

Dioicous, heterothallic, male gametophytes much smaller than female ones. *Antheridia* individually developed inside small, unistratose, brownish purple, flask-like involucre, in acropetal sequence, crowded along stem dorsally. *Archegonia* also enclosed, almost always individually, in much larger, green, flask-like involucre, wall double-layered only in single South African species, *S. stipitatus*; in other species unistratose. *Calyptra* delicate, unistratose around cleistocarpous capsule, 3- or 4-stratose around short, necrotic seta and subspherical foot, disintegrating when spores reach maturity, allowing their release, when flask wall also decays. *Spores* in permanent tetrads in South African species, large, external face covered with ridges; in some extra-South African species separating at maturity, the spore ornamentation areolate to lamellate. *Nutritive cells* present, but elaters absent.

Sphaerocarpaceae (Dumort.) Heeg in Verhandlungen der kaiserlich-königlichen zoologisch-botanischen Gesellschaft in Wien 41: 573 (1891) ('Sphaerocarpeae'); Müll.Frib.: 310 (1951–1958); S.W.Arnell: 8 (1963); R.M.Schust.: 810 (1992).

Tribe *Sphaerocarpeae* Dumort. 13: 163 (1874).

Subfamily *Sphaerocarpoideae* Schiffn.: 50 (1893); Engl.: 49 (1898).

The Sphaerocarpineae include only the single family, Sphaerocarpaceae; hence, the details in the subordinal description are not repeated here.

Sphaerocarpos (Micheli) Boehmer in C.G. Ludwig, Definitiones generum plantarum: 501 (1760); Haynes: 219 (1910); Prosk.: 153 (1954); S.W.Arnell: 8 (1963); R.M.Schust.: 816 (1992). Type: *S. michelii* Bellardi.

Sphaerocarpos Micheli: 4, t. 3 (1729).

Sphaerocarpus Adanson: 15 (1763) [orth. var.]; Steph.: 655 (1899); Müll.Frib.: 310 (1951–1958).

Plants ephemeral, gregarious to scattered; stems once or twice (or more frequently) furcately branching, dorsiventrally flattened, laterally invested with delicate, succubously inserted, leaf-like lobes; ventrally (and apically) with scattered slime papillae; ventrally with smooth, hyaline rhizoids.

Dioicous, strongly heterothallic; gametangia individually enveloped by flask-shaped involucre, small in male plants, but much larger in females, which are sessile or stipitate, wall unistratose, only exceptionally bistratose, eventually containing globose capsule and short seta with foot. Spores remaining in tetrads or separating at maturity, ornamentation reticulate or ridged.

Species in the genus fall into two, well-defined groups that were recently segregated by Schuster (1992).

Key to subgenera of *Sphaerocarpos*

- 1a Sporophytes delicate, sessile on stem or axis; wall of flasks unistratose, without cells projecting as processes on their inner surfaces subgenus *Sphaerocarpos*
- 1b Sporophytes firm, stipitate, but length of stalk variable; wall of flasks bistratose, with inner surface bearing inward-projecting, finger-like cells, rich in chloroplasts subgenus *Austrosphaerocarpos* R.M.Schust.

Proskauer (1954) concluded that the specific epithet *stipitatus* for this species was apt, since such a stalk did not exist in any other species of the genus. The longest stalk that he measured was ± 1.5 mm. Recently, however, Long (1993) reported that in the material from Nepal and Portugal (Sérgio & Sim-Sim 1989), 'the female

flasks have an extremely short basal stalk'. The stalks I measured were also short, only 200–795 µm in length, which would support Long's observation that, 'development of the stipe must be considered variable', hence the minor alteration I made to Schuster's (1992) key to the subgenus *Austrosphaerocarpus*.

***Sphaerocarpus stipitatus* Bisch. ex Lindenb.**, Verhandlungen der kaiserlichen Leopoldinisch-carolinischen deutschen Akademie der Naturforscher 10 (= Nova acta Academiae Caesareae Leopoldino Carolinae germanicae naturae curiosorum 18): 504 i (1837); Haynes: 228 (1910); Prosk.: 144 (1954); Prosk.: 63 (1955); S.W.Arnell: 8 (1963); Sérgio & Sim-Sim: 414 (1989); Long: 77 (1993). Type: Chile, Quillota, *Bertero* 695 (PC, holo.).

Sphaerocarpus berterii Mont.: 39 (1838); Nees: 369 (1838); Mont.: 50 (1839); Gotsche et al.: 595 (1846).

Sphaerocarpus berteroi Mont. orth. mut.; Steph.: 657 (1899); nom. inval., orthographic variant for *S. berterii*.

Plants ephemeral to short-lived, gregarious or scattered; stems once or twice, to repeatedly furcately branching and forming partial rosettes; markedly heterothallic, male gametophytes tiny (Figure 1A, B), antheridial flasks purplish brown, intimately associated with much larger ($\times 10$), light green, female gametophytes. *Stems* somewhat indeterminate, in both sexes prostrate, dorsiventrally flattened, in the middle up to 260–300 µm thick, consisting of (2–)3 or 4 layers of thin-walled, 4- or 5-sided, elongated cells, 112.5–160.0 \times 45–75 µm, ventral cell layer with scattered slime papillae, 37.5–62.5 \times 17.5–22.5 µm, raised on smaller or larger basal cell; above mostly obscured by crowded gametangia, each with a small or large (depending on sex) flask-shaped involucre, produced in acropetal sequence, usually in 2 series; laterally giving rise to delicate, unistratose, translucent, alternate, succubously oriented, leaf-like lobes; ventrally anchored to substrate by rhizoids, all smooth, hyaline, 30–50 µm wide.

Dioicous. *Male plants* with branches (Figure 3A) 1250–1750 \times 525–625 µm, tapering apically, close together and almost parallel to widely divergent, laterally with mostly obscured, leaf-like lobes (Figure 1C, D), fan-shaped, 650–1025 µm long, above 400–975 (–1100) µm wide, narrowing toward base, 100–650 µm wide; upper marginal cells mostly subquadrate, 40–50 \times 47.5–70.0 µm, middle laminal cells long-rectangular, 132.5–145.0 \times 42.5–62.5 µm, basal cells 125.0–137.5 \times 75.0–87.5 µm. *Antheridial involucre*s (Figures 2B; 3B, C) generally in 2 or 3 series along segments, sessile, flask-shaped, 250–280 µm high, apically contracted, opening surrounded by 7 or 8 vertically oriented cells, 45.0–62.5 (–92.5) \times 25–30 µm, their apices projecting somewhat, median sector inflated, width across 180–200 µm, wall unistratose, cells generally 4-sided, sometimes their walls bulging, mostly 50.0–67.5 \times 27.5–45.0 µm. *Antheridia* (Figure 2A) individually nearly completely enclosed by flasks, only apical ones not discharged, ovoid, \pm 125 \times 82.5 µm, raised on short pedicel, up to 57.5 \times 17.5 µm, consisting of uniseriate column of 5 cells.

Female plants pseudodichotomously branching 1–3 times, forming partial rosettes, 4.5–6.5 mm across, sometimes segments simple (Figure 1E) or nearly so, \pm 4.4 \times 2.6 mm, lateral leaf-like lobes (Figure 1F–M) mostly single, occasionally bilobed, obovate, size variable, 1075–2500 \times 625–3375 µm above, narrower below, 275–1125 µm wide; cells at upper margin (Figure 1N) usually isodiametric, 55.0–57.5 \times 50.0–62.5 µm, thin-walled, sometimes cell projecting at angle much larger, \pm 52.5 \times 145 µm, cells at lateral margin 87.5–125.0 \times 30.0–42.5 µm; upper laminal and median cells long-hexagonal, 92.5–200.0 \times 50–70 µm, basal cells 155.0–177.5 \times 55–105 µm. *Archegonial involucre*s often crowded together, obscuring leaf-like lobes (Figure 3D), sessile when first initiated, later stalked (Figure 3E), ellipsoidal or bluntly conical (Figure 2C–E), at maturity 1800–3000 µm high, width 750–1125 µm across widest, basal part, narrowing gradually upwards to mouth and generally more abruptly below towards stalk, mouth (Figure 3F) usually 250–300 µm wide, surrounded by unistratose ring of 16 or more hyaline cells, 100–105 \times 50–60 µm, rounded above and projecting somewhat crenulately; rarely, larger involucre containing 2 sporophytes (Figure 2F), 3625 µm high, at mouth \pm 625 µm wide, 2050 µm wide across basal part; below mouth rest of involucre wall double-layered: outer cells hyaline, chloroplasts absent, long-rectangular above (Figure 2I), 125.0–147.5 \times 40.0–42.5 µm, lower down gradually enlarging (Figure 2H), 5- or 6-sided, 150–300 \times 75–125 µm; inner cells (Figure 2J–L) finger-like, much more numerous, in clusters, rich in chloroplasts, with free, downward curving, papilliform tips, up to 185 \times 32.5 µm in upper part of flask, smaller lower down and often becoming partially destroyed. *Stalk* developing by intercalary growth, length variable, 200–795 µm, width 175–250 µm, in cross section (Figure 2G) mostly with 6 cells across, cells in outer row 30–40 \times 40–60 µm, inner cells in 4 rows, \pm 75 \times 75 µm. *Calyptra* remaining unruptured for a long period enveloping mature capsule, seta and foot (Figure 2M) hyaline, mostly unistratose, cells 4–6-sided, 65–145 \times 65–100 µm, smaller above, where crowned by persistent archegonial neck (Figure 2N) and below, where closely investing seta and foot, here up to 4-stratose. *Archegonial neck* 75–85 \times 30.0–37.5 µm, formed by 6 rows of cells and reportedly (Schuster 1992) with only 2 neck-canal cells. *Capsule* 650–825 µm diam., wall (Figure 2Q) unistratose, lacking thickenings, cells \pm 5-sided, 37.5–65.0 \times 37.5–50.0 µm, densely covered with starch granules, particularly when young; with age their number apparently reduced, subround or oval, 5.0–12.5 \times 5–10 µm. *Seta* (Figure 2O) with 4 cell rows, very short, \pm 100 \times 40 µm, becoming necrotic. *Foot* partly fused with calyptra below, bulbous, \pm 270 \times 220 µm, resting on 'platform' of cells filling basal part of flask, cells 100–170 \times 75–125 µm; in cross section (Figure 2P) centrally with several 'haustorial' cells, roughly triangular, corners rounded, \pm 42.5 µm long, up to 47.5 µm wide across widest part, surrounded by thin layer of non-cellular tissue and then by 2 or 3 rows of hyaline cells, the largest, outermost cells 30.0–37.5 \times 32.5–37.5 µm. *Spores* remaining in tetrads, 87.5–112.5 µm diam., yellow-brown to dark brown; 3 (Figure 4C) or all 4 spores (Figure 4A, B, D, E) of tetrad visible at the same time, joined at thin line in narrow groove (Figure 4F), \pm 2.5 µm wide, ornamentation ridged, with 16–19 minutely

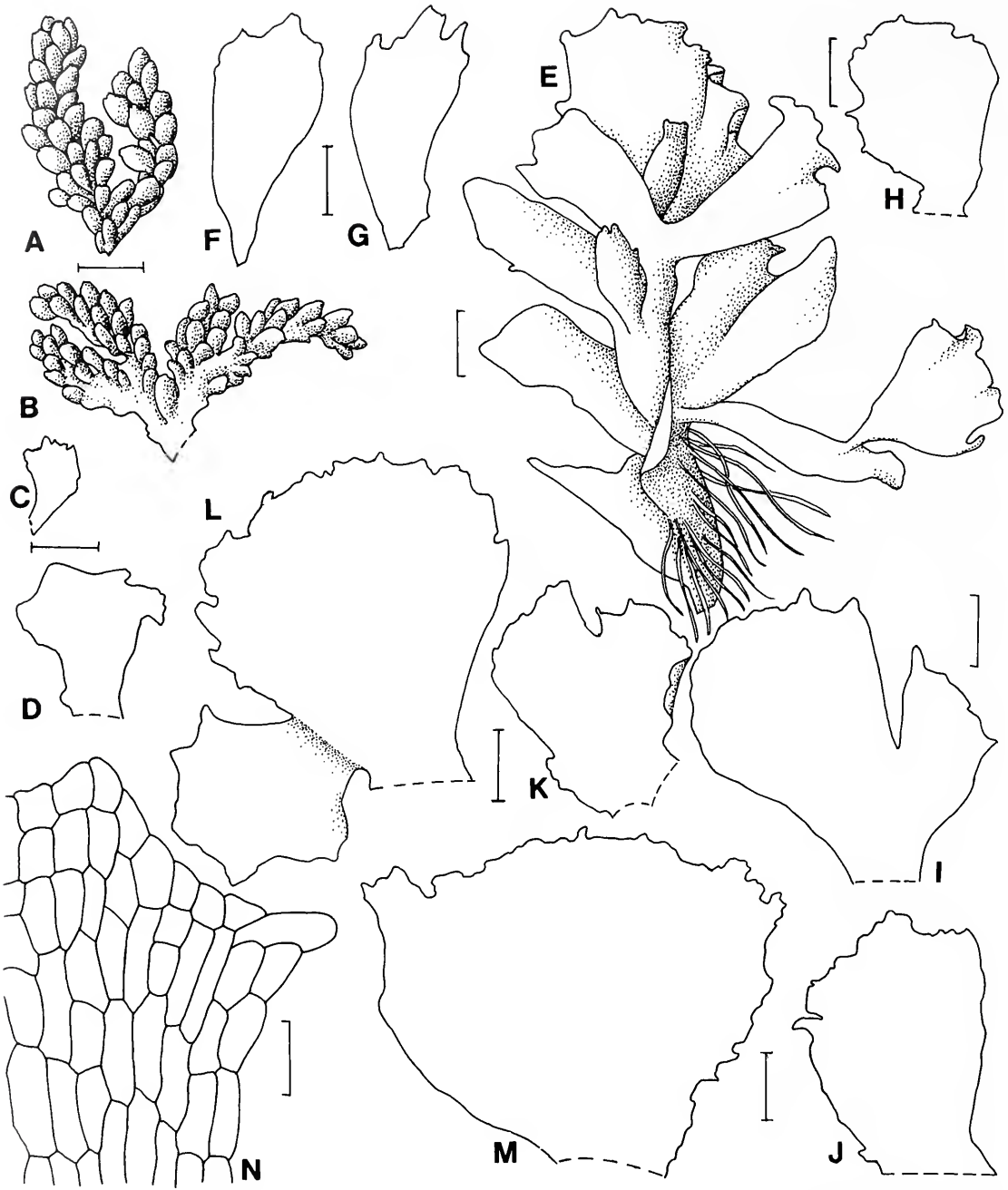


FIGURE 1.—*Sphaerocarpos stipitatus*. A, B, dorsal view of male gametophytes with antheridial involucre; C, D, young male, and older, leaf-like lobes, respectively; E, dorsal view of female gametophyte with stem ('axis') and lateral, leaf-like lobes; F–M, female leaf-like lobes; N, detail of leaf-like lobe. A–N, Koekemoer 1425. Scale bars: A–M, 500 µm; N, 100 µm. Artist: Gillian Condy.

papillate ridges, sometimes branched and up to 10 µm apart, running from centre of distal faces outward and stopping short at groove, rarely forming incomplete areolae. *Nutritive cells* (Figure 2R1–3) generally ovoid, 42.5–50.0 × 30.0–37.5 µm, apparently with several nuclei (4–8), resulting from mitoses and therefore remaining diploid, sometimes 4-celled; although containing starch granules and chloroplasts, their role in nutrition of developing spores not proven. Release of

spores and nutritive cells by disintegration of the capsule wall, then by the calyptra and finally by the wall of the flask.

DISCUSSION

The genus *Sphaerocarpos* has aroused much interest, because sex chromosomes in plants were first found in *S. donnellii* by Allen (1919). Since then, it has been

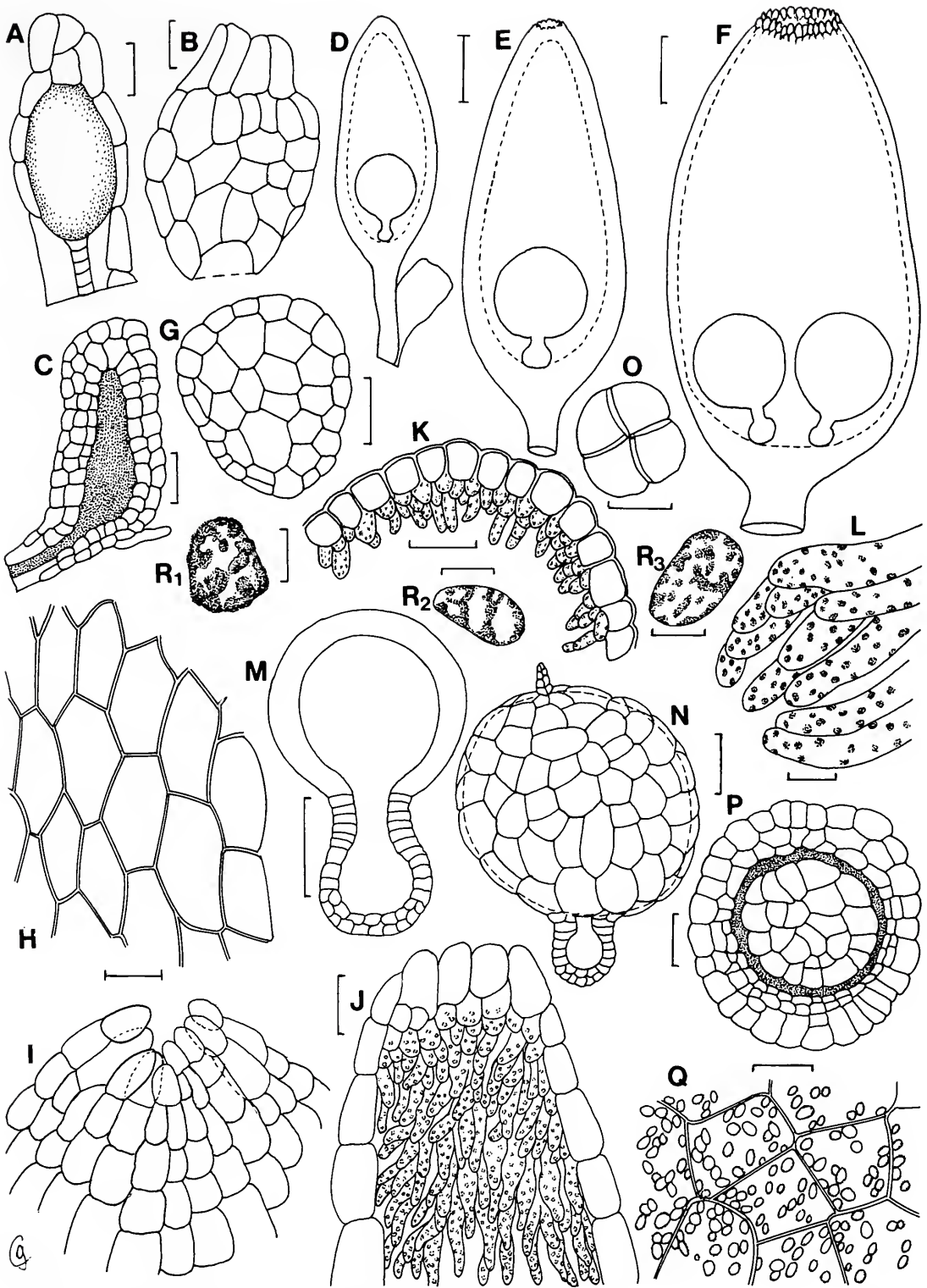


FIGURE 2.—*Sphaerocarpos stipitatus*. A, male involucre containing antheridium partly exposed; B, male involucre; C, archegonium and flask; D, E, older flasks; F, large flask with 2 capsules; G, c/s stalk; H, cells in outer wall of flask (without chloroplasts). I–L, wall of flask: I, mouth and upper part from outside; J, mouth and upper part with papilliform cells from inside; K, c/s with larger, clear outer cells and smaller, inner cells containing numerous chloroplasts; L, inner cells more enlarged. M, younger capsule, with seta and foot enveloped by calyptra; N, calyptra, above with persistent archegonial neck, below covering seta and foot; O, c/s seta; P, c/s foot; Q, capsule wall without thickenings, but covered with starch grains; R₁–R₃, nutritive cells. A–R₃, *Koekemoer 1425*. Scale bars: A–C, L, P, 50 μ m; D–F, 500 μ m; G–K, 100 μ m; M, N, 200 μ m; O, Q, R₁–R₃, 25 μ m. Artist: Gillian Condy.

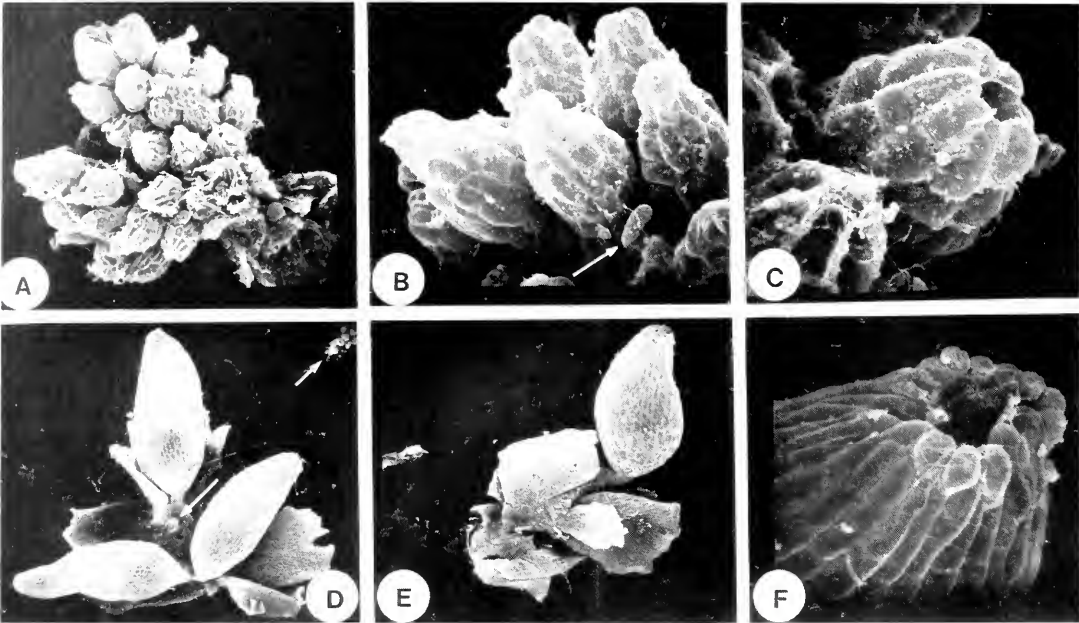


FIGURE 3—*Sphaerocarpus stipitatus*. A, male plant covered with numerous antheridial involucre; B, antheridial flasks, with arrow indicating upper cell of slime papilla; C, mouth of antheridial flask; D, female plant with leaf-like lobes and 3 flasks, 4th flask removed, remainder of its stalk indicated by arrow; at top, right corner tip of male branch covered in flasks, to compare difference in sizes of male and female plants; E, female plant with single flask on longer stalk, partly hidden by leaf-like lobe; F, mouth of female flask. A–F, *Koekemoer 1425*. A, $\times 45$; B, $\times 135$; C, $\times 254$; D, $\times 8.5$; E, $\times 14$; F, $\times 83$.

repeatedly studied with regard to its genetics and cytology; furthermore, a number of cultures have been maintained for lengthy periods of time.

In several aspects, the gametophyte, with its prostrate stem (or axis) and delicate, 2-ranked, succubously insert-

ed leaf-like lobes, resembles *Fossombronina* species, but so-called ‘angle’ leaves at the fork of dichotomies, as described by Proskauer (1954) and Schuster (1992), have not been observed by me in the present study, although I am familiar with them from my work on the Fossombroniaceae (Perold 1999a).

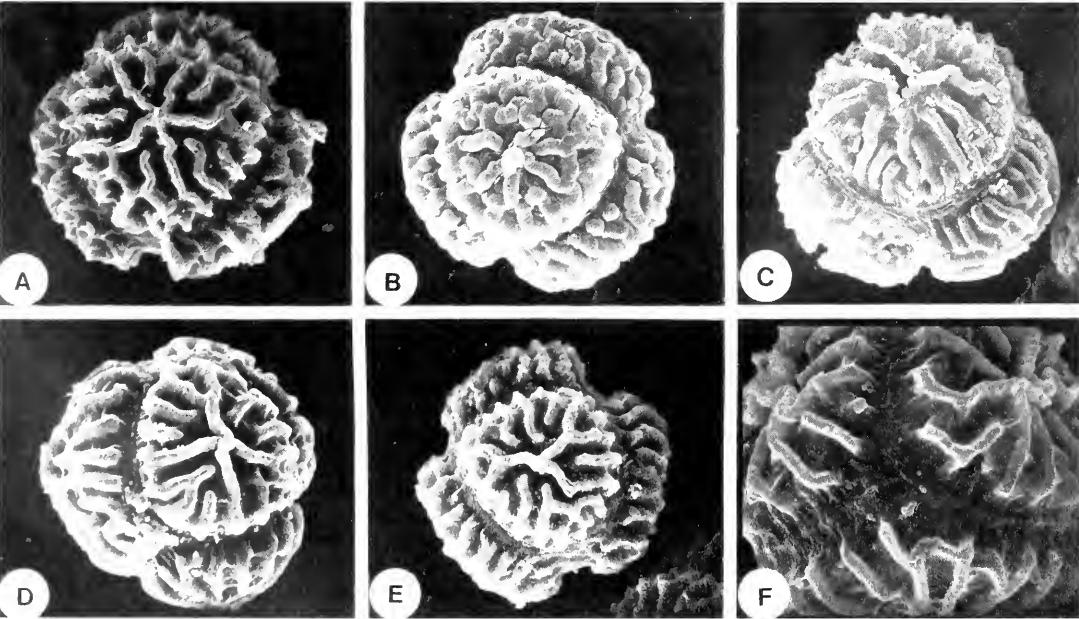


FIGURE 4—*Sphaerocarpus stipitatus*. A–E, spore tetrads; F, groove where 3 of tetrads are joined. A, *E.A.C.L.E. Schelpe 4877* (BOL); B, *Toelken 1978* (BOL); C, *A.S.L. Schelpe 760* (BOL); D, *S.M. Perold 1838*; E, *Koekemoer 1425*; F, *Oliver 8961*. A, D, $\times 366$; B, $\times 439$; C, $\times 374$; E, $\times 347$; F, $\times 682$.

The gametophyte in *Sphaerocarpos* species is delicate and lacks physiological drought resistance (Schuster 1992); it is, nevertheless, adapted to warm and sometimes disturbed areas, with adequate moisture only seasonally and with intervening long, dry periods. It is regarded as an ecological specialist and is a temporary component of vegetation that frequently endures drought in summer. To cope with such an environment, its life cycle is considerably shortened and development of the sporophyte is accelerated; it survives the dry periods as spores, which generally remain in tetrads, eventually giving rise to two male plants in close proximity to two female plants, thus ensuring that fertilisation takes place and that a new generation will ensue.

In using a molecular approach by determining sequences for the 18S-r RNA gene to construct phylogenetic trees of a number of bryophytes, Capesius & Bopp (1997) concluded that the Sphaerocarpaceae diverged early as a separate clade among the Marchantiopsida.

Ecology

In southern Africa, *S. stipitatus* is restricted to the winter rainfall regions of the Northern, Western and Eastern Cape, which experience hot, dry summers (Figure 5). The plants grow at altitudes ranging from sea level to $\pm 1\ 200$ m, on moist, fine-grained, sandy to clayey soils or on mud; at drainage ditches, water courses or on earth banks; under fynbos, short karroid scrub or grass, often together with mosses and *Riccia* species. The localities fall in several different vegetation types, namely Mountain Fynbos, Upland and Lowland Succulent Karoo, as well as Grassy Fynbos (Low & Rebelo 1996). Dates when sporulating material was collected, range from the end of July to early October.

Specimens examined

Britten 58348 (BOL).

Koekemoer 1425 (PRE).

Magill & Schelpe 3961A (PRE).

Oliver 8961 (PRE).

Perold 1838 (PRE).

A.S.L. Schelpe 760 (BOL58344); E.A.C.L.E. Schelpe 4877 (BOL58346), 4918b (BOL58345).

Toelken 1978 (BM) (BOL58347) (ridges rather thicker in the spores from this specimen; see Figure 4B).

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My sincere thanks are extended to Dr D.G. Long for kindly refereeing this paper, to the Curator of BOL for the loan of specimens; to Dr O.A. Leistner for his valuable advice and to my colleagues at NBI for kindly collecting specimens of *S. stipitatus*, and particularly, to Ms M. Koekemoer, Curator of PRE, for collecting and carefully tending live material; also to Ms G. Condy for the drawings; Mrs A. Romanowski for developing and printing the micrographs and to Ms D. Maree for typing the manuscript.

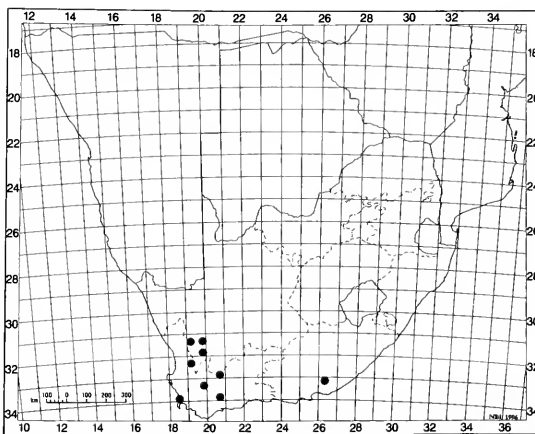


FIGURE 5.—Distribution of *Sphaerocarpos stipitatus* in southern Africa. Pocock specimen not indicated on map (grid reference 3326AD), because I did not examine it.

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FSA contributions 15: Piperaceae

K.L. IMMELMAN*

Herbs, shrubs or rarely small trees, evergreen, often succulent when herbaceous, often epiphytic or lithophytic, sometimes aromatic, erect or scandent; nodes often swollen or jointed; stems with vascular strands distinct and somewhat scattered as in monocots. *Leaves* usually alternate, rarely opposite or verticillate, simple, entire; stipules absent or adnate to petiole. *Inflorescence* a dense cylindrical fleshy spike; spikes may be arranged in an umbel. *Flowers* minute, bisexual or unisexual, without perianth, each flower subtended by a peltate bract. *Stamens* 1–10, hypogynous; filaments usually free; anthers often articulated on the filaments; thecae 2, distinct or confluent. *Ovary* superior, unilocular, with a single basal, erect ovule; stigmas 1–5, short, often brush-like and lateral in *Peperomia*. *Fruit* baccate, with a succulent, thin or dry pericarp, often sunken into succulent rachis. *Seeds* globose, ovoid or oblong in outline, testa membranous or rather fleshy, embryo minute.

A family of about eight genera and over 3 000 species; widespread in warm areas but especially common in South and Central America and in central Asia. There are two genera represented in the FSA area, *Piper* and *Peperomia*.

Various species are the source of pepper, cubebs and various narcotics, and species of both genera are grown as houseplants for their decorative foliage.

Shrubs; anther thecae usually distinct; stigmas 2 *Piper*
Herbs; anther thecae usually confluent; stigma 1 *Peperomia*

1862000 PIPER

Piper L., Species plantarum, edn 1: 28 (1753); L.: 18 (1754); C.DC.: 240 (1869); Benth. & Hook.f.: 129 (1880); Baker & C.H.Wright: 144 (1902–1913); C.H.Wright: 488 (1912); Keay: 84 (1954); Emboden: 91, 129 (1972); R.A.Dyer: 29 (1975); Tebbs: 518 (1993); Verdc.: 1 (1996); Diniz: 25 (1997); Mabb.: 560 (1997). Type: *P. nigrum* L.

Erect or scandent herbs, shrubs or rarely trees; branches terete, jointed at nodes. *Leaves* alternate, entire, sometimes asymmetrical at base, penninerved; stipules adnate to petiole or connate into a leaf-opposed sheath. *Inflorescence* a dense, cylindrical spike, terminal on ends of stems or on leaf-opposed short shoots; bracts sessile, peltate. *Flowers* bisexual, sessile, without perianth. *Stamens* 2; filaments very short; thecae distinct. *Ovary* sessile; stigmas 2, distinct, recurved; ovule solitary, basal. *Fruit* globose, compressed, sessile; pericarp thin and dry.

Characters not applicable in South Africa: *Flowers* unisexual, may be pedicellate. *Stamens* 3 or 4, rarely 5–many; filaments occasionally longer than bracts. *Ovary* rarely stipitate; stigmas up to 5, may be erect. *Fruit* rarely stipitate; pericarp may be succulent.

A large genus of over 2 000 species; in Asia as far east as Japan, in tropical America, with a few species in Africa. A single species, *P. capense*, occurs in southern Africa.

As well as *P. capense*, a second species, *P. borbonense* (Miq.) C.DC., was recorded from the FSA area by Wright (1912). He cited specimens of Verraux and Gueinzus, both without precise locality. Killick (1970) considered that the Gueinzus specimen was probably destroyed during World War II, while the Verraux specimen proved to be a true *P. borbonense*. Killick suggested that the wrong label was placed on this specimen, and certainly no other specimen of this species has been seen from southern Africa by me. Possibly the Gueinzus specimen was either mislabelled or misidentified, but this is now impossible to determine. *P. borbonense* is quite different from *P. capense*, as it is parasitic and dioecious.

Various species of *Piper* are the source of spices and narcotics. *P. nigrum*, originally from India and brought from there to Java, is the source of commercial pepper. The ripened fruit with the pericarp removed gives white pepper, while the more pungent black pepper comes from the unripened fruit milled whole.

In S Asia and the islands of the Indian and Pacific oceans, *Piper betle* leaves are rolled with a piece of betel palm (*Areca catechu*) and lime, and chewed as a mild stimulant. *P. methysticum*, which is closely related to pepper, is cultivated in the Pacific Islands. The roots and lower stem are chewed and used to make a beverage called kava-kava, which has a relaxing effect (Emboden 1972).

Piper capense Lf., Supplementum plantarum 90 (1781); Thunb.: 443 (1823); C.DC.: 339 (1869); C.DC.: 224 (1894); Engl.: 146 (1913); Baker & C.H.Wright: 146 (1902–1913); C.H.Wright: 488 (1912); Eyles: 337 (1915); Keay: 84 (1954); Killick: t. 1583 (1970); Agnew: 88 (1974); Coates Palgrave: 90 (1977).

var. **capense** Verdc.: 5 (1996); Diniz: 27 (1997). Type: Western Cape, growing in forest in Outeniquas and Grootvadersbos, near river, *Thunberg s.n.* (UPS, holo.; microfiche in PRE, No. 713!).

Herb or soft-wooded shrub, rarely a small tree, sometimes scrambling, 0.5–2.5(–3.5) m high; stems swollen at nodes. *Leaves* ovate to very broadly ovate, 70–130 ×

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FIGURE 1.—*Piper capense*: A., habit, $\times 0.87$; B, fruiting inflorescence, $\times 1.75$; C, part of fruiting inflorescence, $\times 5$; D, flower with bract and two stamens, $\times 13$. A, D, Werger 1443; B, Story 4207; C, Strey 9014. Artist: G. Condy.

26–95(–115) mm, palmately 5–7-nerved, apex attenuate, base truncate or cordate, occasionally cuneate, may be symmetrical or asymmetrical, dark glossy green above, paler below, with hairs when young, later only on under-surface along veins, glabrescent above; petiole channeled above, 10–50 mm long; stipules present. *Inflorescence* a slender cylindrical spike, terminating either the main shoot or the short leaf-opposed side shoots, ± 30 –50 mm long (in flower), up to 80 mm long (in fruit). *Flowers* subtended by peltate bracts; stamens 2 or 3; ovary ovoid; style short, with 2 stigmas. *Fruits* compressed-ovoid, with a membranous reddish pericarp. Figure 1.

Occurs in central, western, eastern and southern Africa; in South Africa is found from Northern Province to Eastern Cape, and then disjunctly from the Knysna-Tsitsikamma area as far west as Western Cape: Swellendam, Grootvadersbos (Figure 2). It grows in the understorey of densely shady, moist forests.

Vouchers: Botha & Van Wyk 1017 (PRE); Galpin 10084 (PRE); Meeuse 10005 (PRE); Strey 9340 (NH, PRE); Watt & Brandwyk 1767 (PRE).

The main shoot often ends in an inflorescence or a leaf and growth then continues from a shoot further back. These side shoots may continue to grow but more usual-

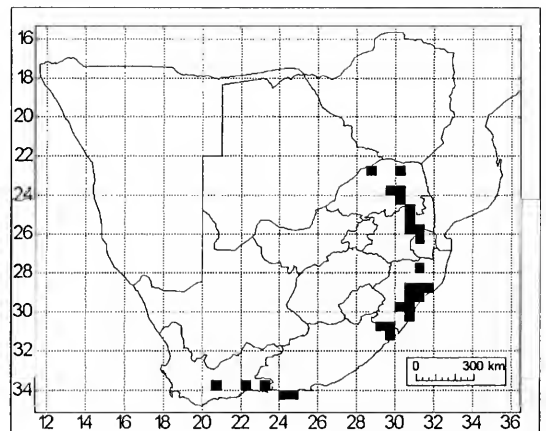


FIGURE 2.—Distribution of *Piper capense* var. *capense* in southern Africa.

ly end in a leaf or sometimes in an inflorescence. When they do end in a leaf, the leaves of the plant may appear superficially to be opposite rather than alternate, but careful examination will show the presence of the stipule or of the scar left where the stipule has abscised. The stipules may either be deciduous or else clasp the petiole.

The fruits have a pleasant spicy smell rather like that of cloves; this intensifies when they are boiled. They have been recorded as having been used as a spice in the past but, as far as is known, are no longer so used.

1866000 PEPEROMIA

Peperomia Ruiz & Pav., Flore peruviana et chilensis prodromus: 8 (1794); C.DC.: 391 (1869); Benth. & Hook.f.: 132 (1880); Baker & C.H.Wright: 147 (1902–1913); C.H.Wright: 489 (1912); Metcalf & Chalk: 1120 (1950); Keay: 81 (1954); Düll: 56 (1973); R.A.Dyer: 30 (1975); Van Jaarsv.: 67 (1992); Tebbs: 519 (1993); Verdc.: 9 (1996); Diniz: 29 (1997); Mabb.: 540 (1997). Type: *P. secunda* Ruiz. & Pav.

Annual or perennial succulent herbs, ascending or prostrate; branches jointed at nodes. *Leaves* alternate, opposite or verticillate, entire, palmately or penninerved; stipules absent. *Inflorescence* a cylindrical spike, terminal or axillary, solitary or aggregated. *Flowers* bisexual, sessile on thickened rachis, without perianth, with short-stalked peltate bracts. *Stamens* 2; filaments short; anther thecae 2, confluent. *Ovary* sessile; stigma undivided, usually penicellate; ovule solitary, basal. *Fruit* minute, globose or ellipsoid; pericarp thin and dry.

Characters not applicable in South Africa: species may be a subshrub or climber.

A genus of about 1 000 species, cosmopolitan in warm areas, especially America. In Africa there are 18 species. Five species are recorded from the FSA area by Düll, but only four are accepted in this treatment.

The species excluded from this treatment is *P. pellucida* (L.) Humb., Bonpl. & Kunth. Düll (1973) cited only one specimen from our area, *Beyrich 99* (B; Beleg durch Bomben vernichtet), from Pondoland, which was probably destroyed in Berlin. The same specimen was quoted by Wright (1909) under the name *P. nana* (a synonym of *P. pellucida*), but he did not indicate that he saw the specimen, as was his practice with all other specimens seen. The description is a direct translation from De Candolle (1869), where *P. nana* was originally described. Baker & Wright (1909) did not record *P. pellucida* from further south than the Zambesi in Mozambique, and it is possible that *Beyrich 99* was misidentified. No specimens of *P. pellucida* from within the FSA area have been seen by me, and it has therefore been decided to exclude it from this treatment. The species is annual, with the leaves alternate, glabrous, cordate at the base, about as wide as long, and widest below the middle.

Key to species

- 1a Leaves ± ovate in whorls of 3 or 4 at nodes; stems succulent; flowers densely crowded on rachis 1. *P. tetraphylla*
- 1b Leaves 1 or 2 at nodes; flowers usually loosely arranged along the axis or, if dense, then leaves orbicular and stems not succulent:
 - 2a Leaves opposite, pilose 4. *P. blanda*
 - 2b Leaves mostly alternate, may be opposite below an inflorescence, glabrous or pilose:
 - 3a Leaves orbicular, occasionally broadly ovate, 4–10 mm long; stems prostrate and non-succulent; fertile portion of inflorescence 2–6 mm long 2. *P. rotundifolia*
 - 3b Leaves elliptic, ovate or obovate, 8–50 mm long; stems succulent, usually ascending; fertile portion of inflorescence 10–45 mm long 3. *P. retusa*

1. **Peperomia tetraphylla (G.Forst.) Hook. & Arn.**, The botany of Captain Beechey's Voyage: 97 (1841); Yuncker: 188 (1962); Düll: 72 (1973); Bond & Goldblatt: 355 (1984); Van Jaarsv.: 68 (1992); Verdc.: 12 (1996); Diniz: 29 (1997). Type: Society Islands, *Forster s.n.* (GOET, holo.; K, iso.).

Piper tetraphyllum G.Forst.: 5 (1786).

Piper reflexum L.f.: 91 (1781); Thunb.: 443 (1823). *Peperomia reflexa* (L.f.) A.Dietr.: 180 (1831) non Humb., Bonpl. & Kunth (1816); C.DC.: 451 (1869); Hook.f.: 99 (1890); Baker & C.H.Wright: 155 (1902–1913); C.H.Wright: 490 (1912); Compton: 171 (1976). Type: Western Cape, Outeniqua Mountains, in woods, among mosses on tree trunks, *Thunberg s.n.* (UPS, holo.; microfiche in PRE No. 752!).

Peperomia reflexa forma *capense* Miq.: 169 (1843). *P. reflexa* var. *capense* (Miq.) C.DC.: 451 (1869); C.H.Wright: 490 (1912); Batten & Bokelmann: 57, t. 50.1 (1966). Syntypes: Western Cape, Cape Peninsula, *Drège s.n.* (not found); Eastern Cape, near Uitenhage, *Verraux 1831* in hb. Delessert (G!); Western Cape, Hangklip, *Mund & Maire s.n.* (not found); Bourbon Island, *Richard in Paris Mus. hb. 707* (P!); Mauritius, Aub. du Petit Thours (not found).

Micropiper pusillum Miq.: 62, t. 5, fig. B (1839). Type: Java, Tjirebon Province, Tjerimai Mountain, upper slopes on tree trunks, *Blume s.n.* (not found).

Succulent herb; stems ascending to suberect (Figure 3E), rooting at nodes and forming a mat. *Leaves* in whorls of 3 or 4, succulent, broadly rhomboid-ovate to ovate, glabrous, 7–15(–25) × 5–11(–14) mm, base and apex rounded, faintly 3-veined from base, may have 3 pale stripes along veins, dark green above and paler to grey-green below, may be punctate below; petiole 1.5–4.0 mm long. *Inflorescence* terminal only, fertile portion 7–11 mm long (in flower), 13–20(–25) mm long (in fruit). *Flowers* with bracts ± 0.3 mm diam. *Fruit* ± 1 mm long, glanduliferous, long-ellipsoid, with pseudocupule at base.

Pantropical; in southern Africa is found in a number of localities in Northern Province, North-West, Mpumalanga, Gauteng, Swaziland, KwaZulu-Natal, Lesotho and in Eastern and Western Cape, from East Griqualand to Bredasdorp (Figure 4). Epiphytic or lithophytic, often growing among mosses.

Vouchers: *Compton 26918* (PRE); *Gibbs Russell 3824* (PRE); *Meeuse 10355* (PRE); *Scheepers 69* (PRE); *Van Wyk & Theron 4534* (PRE).

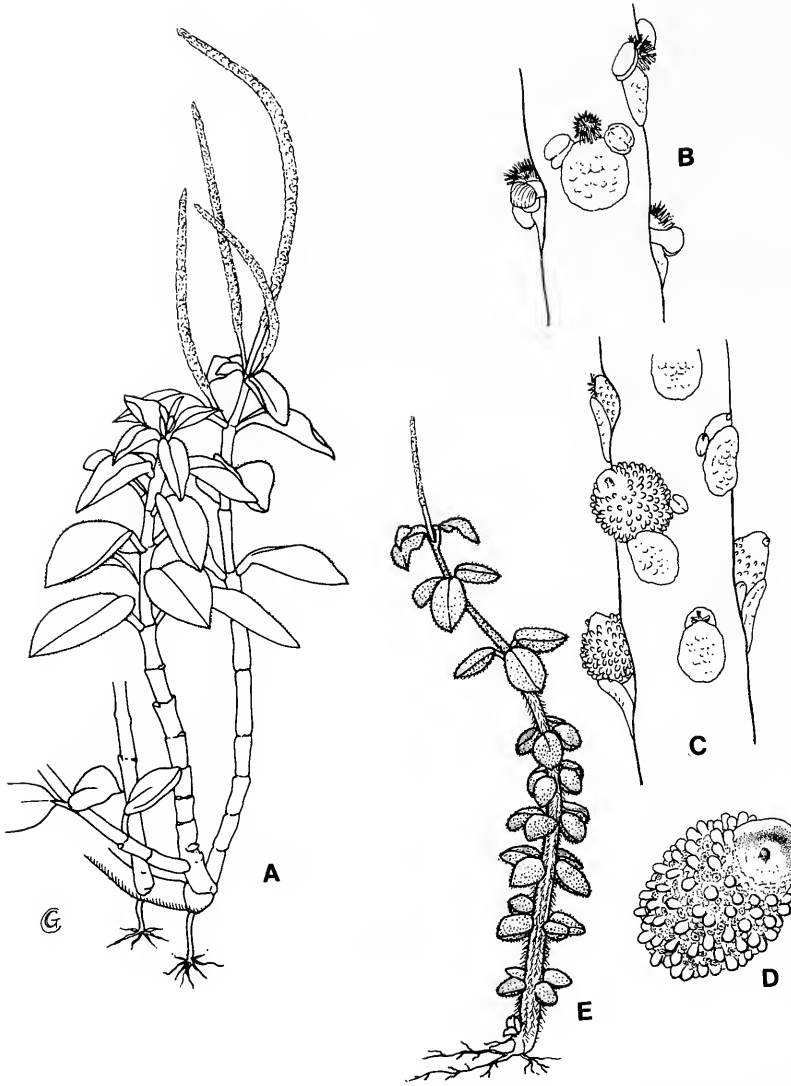


FIGURE 3.—A–D, *Peperomia blanda*, Hardy 3991: A, habit, $\times 0.88$; B, flowering inflorescence, $\times 13$; C, fruiting inflorescence, $\times 13$; D, fruit, $\times 26.6$. E, *Peperomia tetraphylla*, Venter 3786: habit, $\times 0.88$. Artist: G. Condy.

2. *Peperomia rotundifolia* (L.) Humb., Bonpl. & Kunth, Nova genera et species plantarum 1: 65 (1816); Keay: 83 (1954); Düll: 85 (1973); Van Jaarsv.: 68 (1992); Verdc.: 12 (1996); Diniz: 33 (1997). Iconotype: America Calidiore (Martinique), Plumier, Traités des Fougères de l'Amérique 52, t. 69 (1693).

Piper rotundifolium L.: 30 (1753).

Herb; stems slender, trailing, not succulent, rooting at nodes. Leaves alternate, succulent, orbicular or sometimes broadly obovate, glabrous or pilose, 4–10 \times 3–7(–10) mm, apex rounded to emarginate, base rounded to broadly cuneate; petiole 1–3 mm long. Inflorescence axillary, short and dense, 2–6 mm long (in flower). Fruit not seen.

Found in South America and the southern USA., in Africa, the Comores and Madagascar; within South Africa it is rare and restricted in distribution to southern KwaZulu-Natal and Eastern Cape (Figure 5). It is epiphytic or lithophytic.

Vouchers: Flanagan 1821 (PRE); Pegler 763 (PRE); Strey 5823, 6648 (PRE); Venter 883 (PRE).

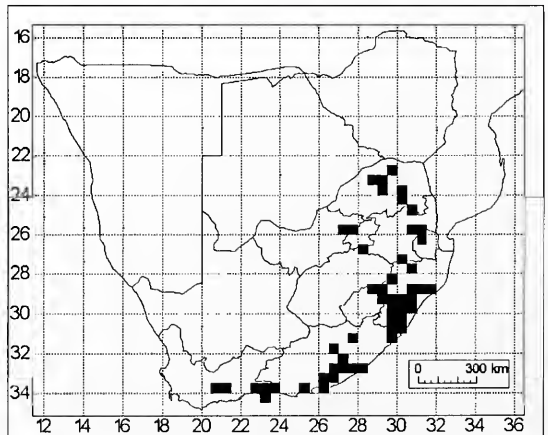


FIGURE 4.—Distribution of *Peperomia tetraphylla* in southern Africa.

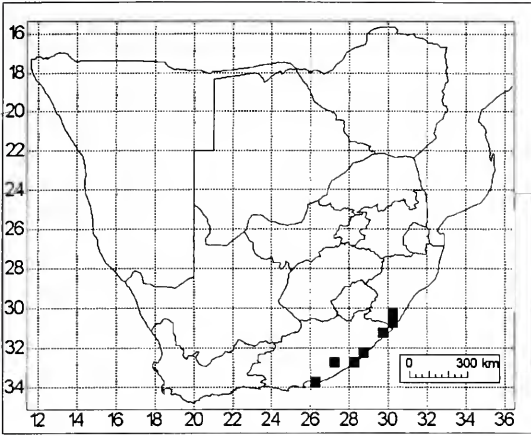


FIGURE 5.—Distribution of *Peperomia rotundifolia* in southern Africa.

3. *Peperomia retusa* (L.f.) A.Dietr., Species plantarum 1: 155 (1831); C.DC.: 446 (1869); C.H.Wright: 491 (1912); Marloth: 128 (1913); Keay: 82 (1954); Düll: 89 (1973); Compton: 171 (1976); Goldblatt in Bond & Goldblatt: 355 (1984); Van Jaarsv.: 68 (1992); Verdc.: 13 (1996); Diniz: 33 (1997). Type: Cape Province, in woods, among mosses on tree branches and on rocks, *Thunberg s.n.* (UPS, holo.; microfiche in PRE no. 754!).

Piper retusum L.f.: 91 (1781); Willd.: 165 (1797); Thunb.: 443 (1813).

Peperomia retusa var. *ciliolata* C.DC.: 447 (1869); C.H.Wright: 491 (1912). Type: Diaboli Mountain, *Fischer s.n.* (not seen, LE vide Düll). It is uncertain whether this locality is American or South African. There is a Mount Diablo in California, on the mainland opposite San Francisco, or it may refer to Devils Peak, Cape Town. No collector by the name of Fischer is known to have been in South Africa, according to Dr L.E.W. Codd (pers. comm.).

Peperomia retusa var. *alternifolia* C.DC.: 446 (1869). Type: Cape Province, *Ecklon & Zeyher s.n.* (B, holo.).

Peperomia bachmannii C.DC.: 227 (1894); C.H.Wright: 491 (1912). *P. retusa* var. *bachmannii* (C.DC.) Düll: 90 (1973). Type: KwaZulu-Natal, Pondoland, *Bachmann 419* (B, holo.).

Peperomia rehmannii C.DC.: 227 (1894). Syntypes: Northern Province, Houtbosch, *Rehmann 5969* (not found); Western Cape, Knysna, *Rehmann 489* (Z, holo.).

Peperomia wilmsii C.DC.: 282 (1898). Type: Mpumalanga, Lydenburg, Spitzkop Mountain, *Wilms 1354* (BM!; G!; K!).

Mat-forming herb; stems rooting at nodes, succulent. *Leaves* alternate, obovate or sometimes elliptic, 8–32 × 6–16 mm, succulent, glabrous, apex usually rounded to emarginate, base broadly cuneate to cuneate, dark green, may be slightly discolorous; petiole 3–7(–13) mm long. *Inflorescence* slender with flowers widely spaced, terminal and axillary, 10–25 mm long (in flower), 25–45 mm long (in fruit). *Fruit* ± 1 mm long.

Occurs in tropical and subtropical Africa and Madagascar; in southern Africa it is the most widespread species of the genus, being found from Northern Province, Mpumalanga, Swaziland, KwaZulu-Natal, Eastern and Western Cape in moist areas as far west as

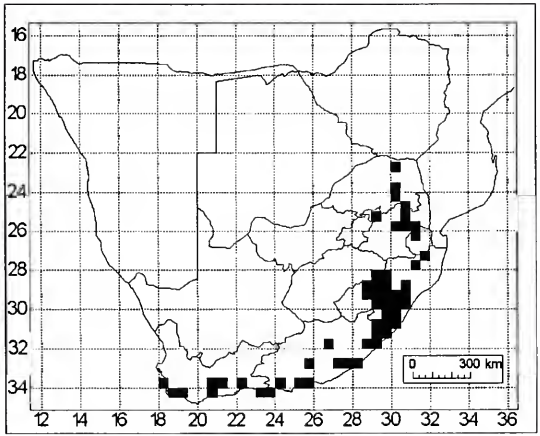


FIGURE 6.—Distribution of *Peperomia retusa* in southern Africa.

the Cape Peninsula, and from sea level to the Drakensberg in Lesotho (Figure 6). Epiphytic or lithophytic.

Vouchers: *Bos 1052* (PRE); *Mohle 262* (PRE); *Venter & Vorster 139* (PRE); *Wager s.n.* (PRE30235); *Zeyde 131* (PRE).

Düll divides the species into three varieties, two of which, var. *retusa* and var. *bachmannii*, occur within the FSA region. The characters he gives as differing, however, show considerable intergradation, and it has therefore been decided here not to keep the two varieties separate.

4. *Peperomia blanda* (Jacq.) Humb., Bonpl. & Kunth, Nova genera et species plantarum 1: 67, t. 3^o (1816); Verdc.: 18 (1996). Type: specimen grown at Schoenbrunn, Vienna, from seed collected at Caracas, Venezuela, *Jacquin s.n.* (W, holo.; K, photo!).

Piper blandum Jacq.: 211 (1791).

Peperomia leptostachya Hook. & Arn.: 70 (1839–1841).

Peperomia arabica Decne. in Miq.: 121 (1843); C.DC.: 442 (1869); Baker & C.H.Wright: 154 (1902–1913); C.H.Wright: 490 (1912); Compton: 171 (1976). Syntypes: Arabie felice, *P.A. Botta s.n.* (P!); KwaZulu-Natal, Port Natal, *Drège s.n.* (G!).

Peperomia blanda var. *leptostachya* (Hook. & Arn.) Düll: 110, Abb. 16 (1973); Van Jaarsv.: 69 (1992). Type: Hawaii, Oahu Island, *Beechey s.n.* (G, holo.; K!).

Semi-erect herb; stems succulent, rooting at lower nodes. *Leaves* opposite, succulent, pilose, ovate, ovate-rhomboid or slightly obovate, 28–50 × 12–31 mm, apex acute to rounded, base cuneate, lower leaves smaller and more rounded; petiole pilose, 6–11 mm long. *Inflorescence* terminal or axillary, slender, with widely-spaced flowers, 20–45 mm (in flower), 22–145 mm (in fruit). *Bracts* ± 0.6 mm diam. *Fruit* ± 1 mm long. Figure 3A–D.

Pantropical; is the most common *Peperomia* species in Central and South America, but less common in Africa. In southern Africa it occurs from Northern Province, Mpumalanga, Swaziland, KwaZulu-Natal to Eastern Cape (Figure 7). It is lithophytic, rarely epiphytic, growing on cliffs and in pockets of soil among rocks.

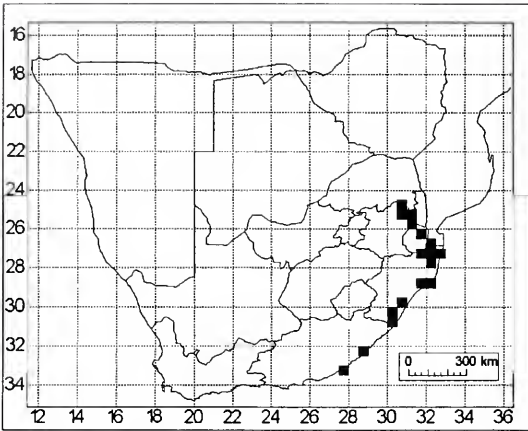


FIGURE 7.—Distribution of *Peperomia blanda* in southern Africa.

Vouchers: Buitendag 470 (PRE); Codd 7029 (PRE); Hemm 539 (PRE); Schweickerd 1425 (PRE); Venter 4577 (PRE); Ward 4110 (PRE).

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FSA contributions 16: Sphenocleaceae

W.G. WELMAN*

Annual glabrous hygrophytic herbs. *Stems* erect or decumbent, somewhat succulent and spongy, usually swollen with aerenchymatous tissue at base, lower submerged part with a pithy covering. *Leaves* alternate, simple, entire, venation pinnate, particularly visible on lower surface; stipules absent. *Inflorescences* terminal, densely spicate, acropetal. *Flowers* small, bisexual, regular, subtended by 1 bract and 2 bracteoles. *Calyx* persistent; tube hemispherical, adnate to ovary; lobes 5, rounded, shortly connate, imbricate. *Corolla* campanulate-urceolate, perigynous, caducous; lobes 5, imbricate. *Stamens* 5, inserted on corolla tube, alternating with petals; filaments very short, dilated at base; anthers short, free, suborbicular, 2-theous, dehiscing longitudinally. *Ovary* semi-inferior, 2-locular; style 1, very short, glabrous; stigma capitate, slightly 2-lobed; ovules very numerous, anatropous, attached to a large spongy stipitate axile placenta. *Fruit* a membranous, 2-locular, depressed-globose, circumscissile capsule (pyxidium); operculum carrying away calyx lobes. *Seeds* very numerous, minute, oblong; testa irregularly plicate-costate; endosperm scanty or absent; embryo axile, straight, subterete.

A close relationship between *Sphenoclea* and the Campanulaceae has been suggested for a long time. Most systematists have treated the genus either as a member of the Campanulaceae (Dahlgren 1983), or as a closely related monogeneric family (Monod 1980; Cronquist 1988). *Sphenoclea* is separable from the Campanulaceae by the imbricate aestivation of the corolla lobes, the circumscissile capsule, the absence of a secondary pollen presentation mechanism, the glabrous style, and by the apparent absence of latex canals.

Airy Shaw (1948, 1968) regarded this family as an isolated group, probably marginally related to the Centrospermae, e.g. *Phytolacca* (habit, anatomy) and perhaps also to the Primulaceae (circumscissile capsules). However, Subramanyam (1950) had shown that embryological and anatomical features reveal important differences between *Sphenoclea*, Phytolaccaceae and Primulaceae. Cosner *et al.* (1994) suggested a position for *Sphenoclea* near the Hydrophyllaceae in the Solanales-Boraginales, but that family has a late sympetaly. Erbar (1995) did SEM-investigations on the floral development of *S. zeylanica* and concluded that the early sympetalous corolla justifies a position of the Sphenocleaceae near the Campanulales-Asterales, to which the family is usually aligned, whereas it is separable from these orders by the absence of a secondary pollen presentation mechanism. Secondary pollen presentation is one of the characters that help to define the Campanulales-Asterales complex. The family may be more

primitive than the Campanulaceae and Gustafsson & Bremer (1995) suggested that *Sphenoclea* does not belong in or near the Asterales, but rather in the other main branch of the Asteridae. The Angiosperm Phylogeny Group (led by K. Bremer, M.W. Chase & P.F. Stevens) concluded in 1998 that the Sphenocleaceae, together with the Convolvulaceae, Hydroleaceae, Montiniaceae and Solanaceae form the Solanales which belong to the Euasterids I; this seems to be strongly supported by molecular data.

8680000 SPHENOCLEA

***Sphenoclea* Gaertn.**, De fructibus et seminibus plantarum 1: 113, t. 24/5 (1788) nom. cons.; Hemsl.: 480 (1877); Hepper: 307 (1963); Airy Shaw: 1 (1968); Thulin: 1 (1973); C.D.K.Cook *et al.*: 533 (1974); R.A.Dyer: 643 (1975); Thulin: 116 (1983); C.D.K.Cook: 217 (1990); Retief & P.P.J.Herman: 624 (1997). Type: *Sphenoclea zeylanica* Gaertn.

Characters of the family.

Two species have been described, namely *S. zeylanica* Gaertn., which is almost pantropical but probably introduced and naturalised in the Americas and southeast Asia, and *S. dalzielii* N.E.Br. (1912) which is endemic to West Africa from Senegal to the Central African Republic. This species, like *S. zeylanica*, grows in wet places, but is a straggly herb with sessile obovate-elliptic leaves. The generic name *Sphenoclea* (Greek) is derived from *spheno* (wedge-shaped, sphenoid) and *kles* (abundance of), presumably referring to the flowers, while the species name *zeylanica* refers to Ceylon (Sri Lanka) where the type was collected. Common name: soapweed; Clark 482 (PRE).

***Sphenoclea zeylanica* Gaertn.**, De fructibus et seminibus plantarum 1: 113, t. 24/5 (1788); Hemsl.: 481 (1877); Hepper: 307, t. 272 (1963); Roessler: 138 (1966); Airy Shaw: 1, t. 1 (1968); Thulin: 2, t. 1 (1973); Thulin: 116, t. 20 (1983); C.D.K.Cook: 363, t. 367 (1996); Retief & P.P.J.Herman: 624 (1997). Type: Ceylon, collector unknown (L, holo.).

Roots numerous, long, cord-like, tenuous, orange. *Stems* stout, hollow, erect, up to 1.5 m tall, often much branched. *Leaves* pale grey-green, linear-lanceolate to oblong-lanceolate, base attenuate, apex acute to obtuse, up to 50 × 150 mm; petiole up to 30 mm long. *Spikes* cylindrical-conical, ± 10 mm diam. and up to 120 mm long, but usually much shorter, narrowed at apex; peduncle up to 80 mm long. *Bracts* and *bracteoles* spatulate to oblanceolate-spatulate, tips arched over flowers except at anthesis. *Flowers* densely crowded, though usually only a few open at a time, rhomboid or hexago-

* National Botanical Institute, Private Bag X101, 0001 Pretoria.
MS. received: 1998–12–15.

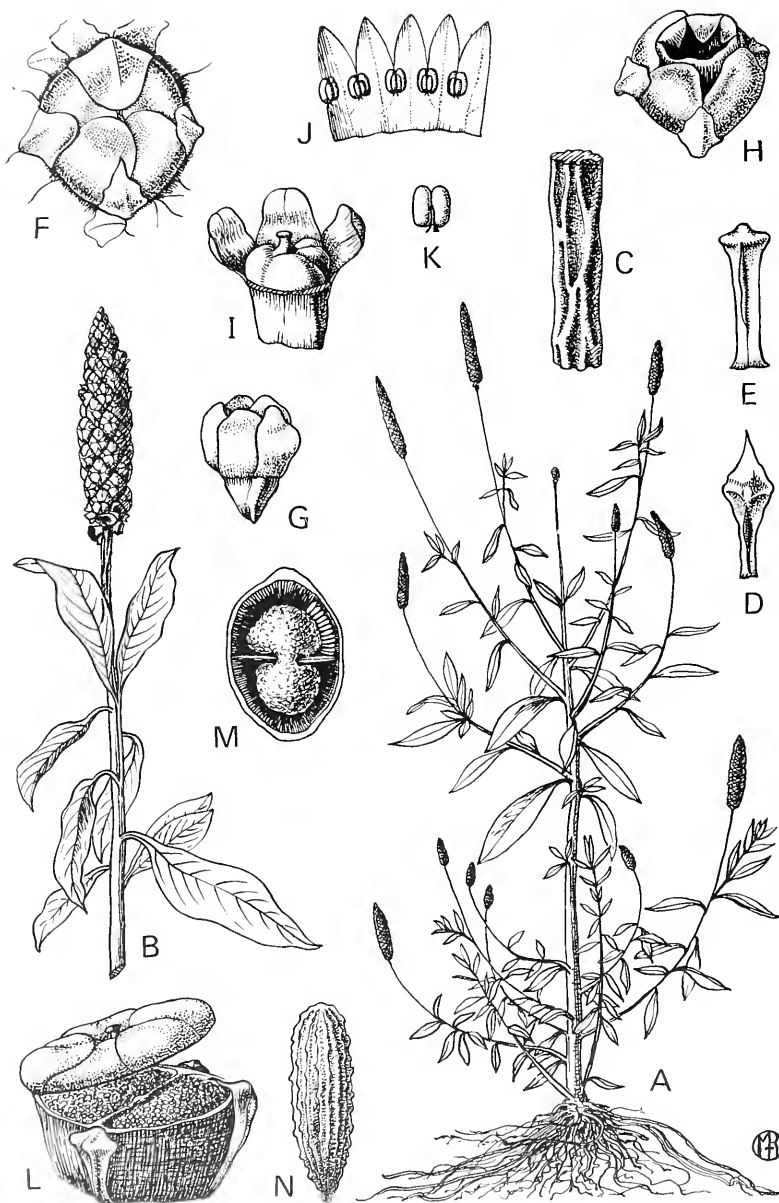


FIGURE 1.—*Sphenoclea zeylanica* Gaertn. A, habit; B, part of flowering branch; C, rachis of inflorescence, showing scars left by fallen capsules; D, bract; E, bracteole; F, flower bud, apical view; G, bud beginning to open, side view; H, flower, showing opening corolla, oblique view; I, gynoecium and calyx, with two sepals removed, showing cuculate base; J, corolla opened out; K, stamen; L, fruit partly dehiscent; M, t/s fruit; N, seed. B, N, Milne-Redhead & Taylor 7463; F, M, Jones FHI 18808; K, Deighton 132a. A, $\times 0.2$; B, $\times 0.9$; C–J, L, M, $\times 5.2$; K, $\times 10.4$; N, $\times 52$. Artist: Olive Milne-Redhead. Reproduced with permission of the Royal Botanic Gardens, Kew.

nal by compression, sessile, wedge-shaped below, attached longitudinally to rachis by a linear base. Calyx lobes grey, broadly triangular, apex obtuse, 1.0–1.5 mm long, ultimately slightly accrescent and connivent. Corolla green, tinged white, yellow, mauve or occasionally purple, ± 4 mm across; lobes 2–4 mm long, ovate-triangular, obtuse or acute, united about half-way, connivent. Filaments shorter than anthers; anthers ± 0.5 mm long. Ovary obovoid, 1.5–2.5 mm long, apex broad, free, truncate. Capsule 4–5 mm diam., dehiscent below calyx lobes, leaving scarious base persistent on rachis. Seeds yellowish brown, ± 0.5 mm long. Figure 1.

In Africa *S. zeylanica* is widespread south of the Sahara (excluding the NE Horn), extending south to northern Namibia, northern Botswana, Swaziland and

also eastern Mpumalanga and northern KwaZulu-Natal in South Africa. Also recorded from Madagascar. Figure 2.

It is autogamous but perhaps also sometimes pollinated by insects. The seeds are dispersed in muddy water and probably also by other means such as in the mud stuck to the feet of birds. In southern Africa, *S. zeylanica* has been recorded on black clay soil, greyish brown sandy clay-loam and also orange-grey sandy loam. It is common in swampy areas, in wet or dry mud on the margins of periodically inundated depressions and flood plains; it is often found along the banks of water courses such as tidal creeks and irrigation channels, also in still, shallow pools. It can be seasonally submerged, emergent or temporarily terrestrial and can tolerate brackish water. *S. zeylanica* has been recorded from grassland and also

among *Acacia* trees; it can be browsed by animals e.g. zebra. It is often gregarious, becoming a troublesome weed in rice fields, but it is also cultivated; young plants are eaten as a vegetable in Java (Indonesia). It grows from about sea level to 1 500 m altitude. *Flowering and fruiting time*: Dec. to May in southern Africa.

Vouchers: Clark 482 (PRE); Giess 15101 (PRE, WIND); Pooley 1609 (NU, PRE); Smith 3710 (PRE, SRGH); Van der Schijff 2593 (KNP, PRE).

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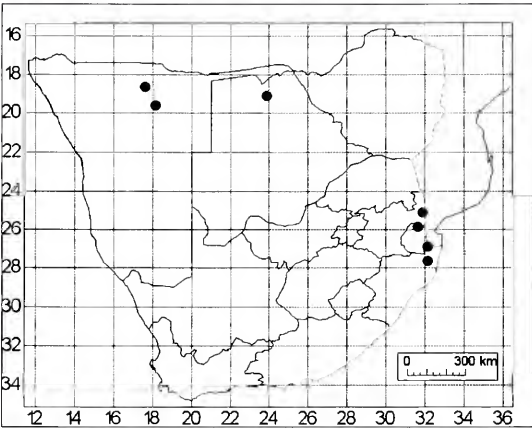


FIGURE 2.—Distribution of *Sphenoclea zeylanica* Gaertn. in South Africa.

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Taxonomic studies in the Aizoaceae from South Africa: three new species and some new combinations

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Keywords: Aizoaceae, new species, new combinations, South Africa, taxonomy

ABSTRACT

Two new species of *Brownanthus*, *B. glareicola* Klak and *B. fraternus* Klak and one new species of *Scopelogena*, *S. bruynsii* Klak are described. *S. gracilis* L.Bolus is reduced to synonymy under *S. verruculata* (L.) L.Bolus. Three new combinations are made: *Antimima excedens* (L.Bolus) Klak, *Erepsia dunensis* (Sond.) Klak and *Hammeria meleagris* (L.Bolus) Klak and full synonymy is given. *Lampranthus maximilianii* (Schltr. & A.Berger) L.Bolus is transferred back to *Braunsia maximilianii* (Schltr. & A.Berger) Schwantes and the identity of *Ruschia polita* L.Bolus is discussed. The taxonomic position of *Mesembryanthemum purpureostylum* L.Bolus is clarified.

Antimima N.E.Br.

This genus was described by N.E. Brown (1930) and later amended by Dehn (1989). Recently about 100 species were moved from *Ruschia* Schwantes to *Antimima* (Hartmann 1998a). However, no revision of the species is available. Although species of *Ruschia* and *Antimima* were for many years included in one genus, they are thought to be unrelated, due to differences in the morphology of their respective capsules. *Antimima* has capsules of the *Leipoldtia* type. These have relatively large, stalked closing bodies, which is considered to be an apomorphy for the *Leipoldtia* group (Hartmann 1991). Whereas all other genera with a *Leipoldtia* type of fruit are multilocular, capsules of *Antimima* are always 5-locular. As a consequence of this circumscription of *Antimima*, a further species is now moved from *Ruschia* to *Antimima*.

Antimima excedens (L.Bolus) Klak, comb. nov.

Ruschia excedens L.Bolus, Notes on Mesembryanthemum and allied genera part 3: 278 (1954). Type: South Africa, Vanrhynsdorp Div., Knersvlakte, Sept. 1950, Meyer SUG12505, sheet 3 (BOL, lecto., here designated).

Braunsia Schwantes

Braunsia is a small genus of about four or five species which is thought to be related to the *Lampranthus* group (Hartmann 1991). The echinate seeds and leaves that are fused for a quarter to half of their length, with white, cartilagenous margins, were so far considered to be the main characteristics of the genus.

The lack of echinate seeds in one of the species, *Braunsia maximilianii*, prompted L. Bolus (1965) to place it rather in *Lampranthus* N.E.Br., which never has echinate seeds. This view stood in contrast to the earlier opinion of N.E. Brown (1929). He considered the pres-

ence or absence of echinate seeds to be unimportant in terms of the genus boundaries, since he had noticed that this character is found in completely unrelated taxa.

Recent investigations now confirm the views of Brown. Apart from the morphology of the flowers and leaves, which are typical for *Braunsia*, the morphology of the capsules excludes this species from *Lampranthus*. In contrast to *Lampranthus*, where the expanding keels always diverge from the base, those of *Braunsia* are parallel for most of their length and only diverge towards the tips. In addition, the covering membranes in *Lampranthus* are always complete and more or less firm, often with additional closing devices below the covering membranes. In *Braunsia* the covering membranes only cover the locules partly, are fairly flexible and do not have any additional closing devices. The capsules of *Lampranthus maximilianii* were found to be typical of species of *Braunsia* in all these details. Therefore the older name, *Braunsia maximilianii* is re-instated here.

Braunsia maximilianii (Schltr. & A.Berger) Schwant. in Gartenwelt 32: 644 (1928a).

Mesembryanthemum maximiliani Schltr. & A.Berger: 633 (1922). *Echinus maximilianii* (Schltr. & A.Berger) N.E.Br.: 57 (1929). *Lampranthus maximilianii* (Schltr. & A.Berger) L.Bolus: 172 (1965). Type: Pakhuisberg, 12 Aug. 1897, Schlechter 10817 (B, holo.; BOL!, GRA!).

Mesembryanthemum apiculatum var. *mutica* L.Bolus: 149 (1913). Type: Gifberg, Sept. 1911, Phillips 7664 (BOL, holo.!).

M. phillipsii L.Bolus: 5 (1925). Type: Schlechter 10817 (B; BOL!, holo.; GRA!, iso.).

M. binum L.Bolus: t. 263 (1927), non N.E.Br. Type: Vanrhynsdorp, Rood NBG1249/23 (BOL, holo.).

Specimens examined

WESTERN CAPE.—3118 (Vanrhynsdorp): Gifberg Plateau, (–DC), *Acocks* 14897 (BOL); plateau between Matsikamma and Gifberg, (–DC), *Esterhuysen* 30750 (BOL); Nardouw, (–DD), *L. Bolus* s.n. (BOL); Cederberg, Kraaibosberg, (–DD), *Klak* 437 (BOL). 3119 (Calvinia): top of Vanrhyn's Pass, (–AC), *Esterhuysen* 7773 (BOL); entrance to Oorlog's Kloof, (–AC), *L. Bolus* BH19232 (BOL);

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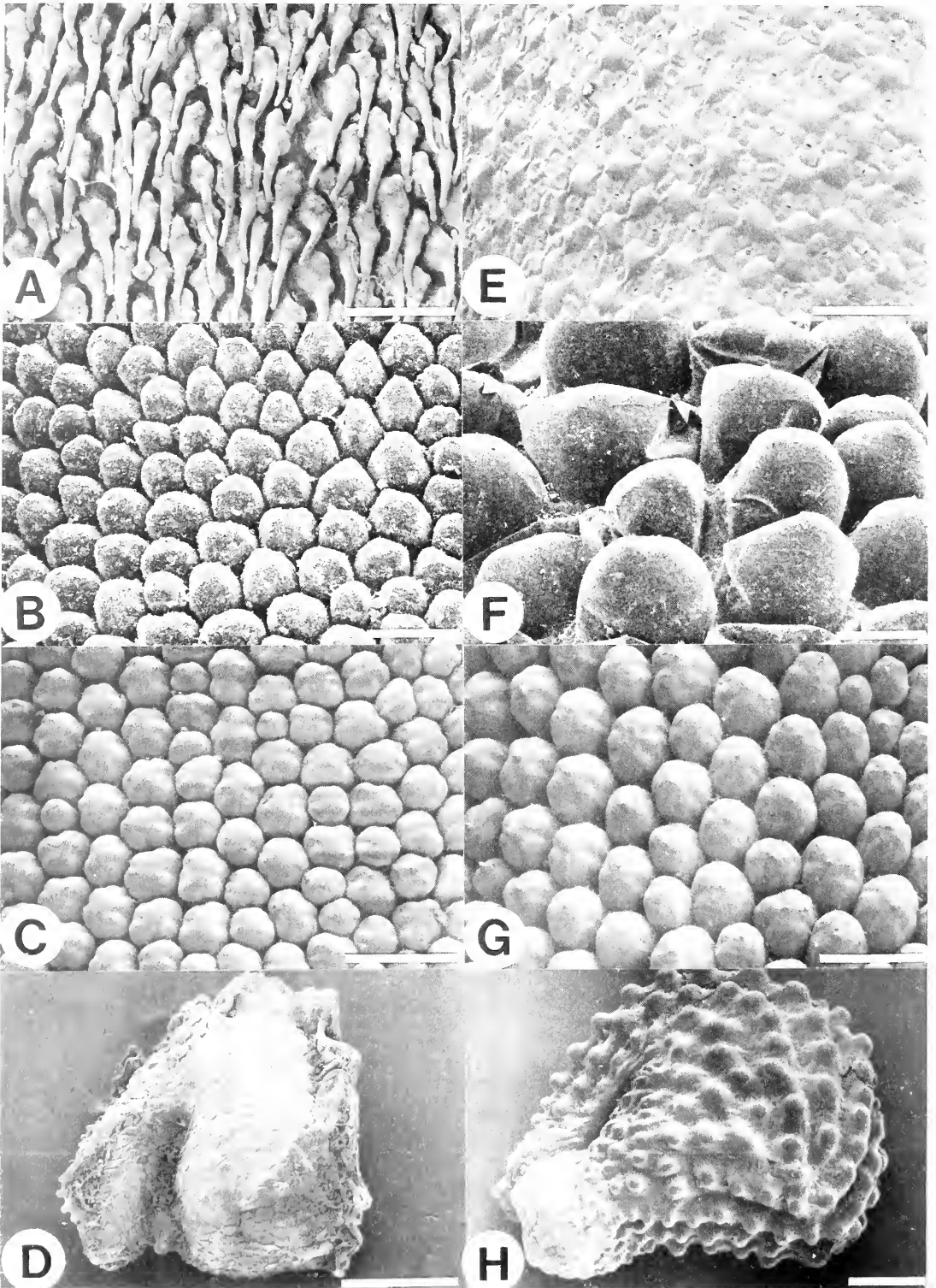


FIGURE 1 —Epidermal surface of *Brownanthus*. A–C: stems, E–G, leaves. A, E, *B. glareicola*, Klak 457; B, F, *B. corallinus*, Klak 64; C, G, *B. fraternus*, Klak 171. D, H, seeds of *Brownanthus*: D, *B. glareicola*, Klak 457; H, *B. fraternus*, Klak 171. Scale bars: B, F, 200 μ m; A, C, E, G, H, 250 μ m; D, 500 μ m.

Nieuwoudtville, (–AC), *E.E. Galpin s.n.*, (BOL), 3218 (Clanwilliam): northeast of Pakhuis Pass, (–BB), *Esterhuysen 32202* (BOL).

Note: the name ‘maximilianii’ is spelt here with ‘ii’ since ‘Maximilian’ is assumed not to be a latinized name and therefore ‘maximiliani’ needs to be corrected by adding an ‘i’ (ICBN Art. 60.11).

Brownanthus Schwantes

Brownanthus is one of 11 genera placed in the sub-family Mesembryanthemoideae. Apart from *Psilocaulon* N.E.Br., *Aptenia* N.E.Br. and *Aspazoma* N.E.Br., it is one of the few genera in the Aizoaceae in which stem succulence has developed (Bittrich 1986). At present ten species are recognised (Pierce & Gerbaulet 1997). The main characteristics of the genus are that the sepals remain upright throughout anthesis, the white or cream-coloured flowers never possess any filamentous staminodes and the lower part of the capsule is shallowly bowl-shaped (Ihlenfeldt & Bittrich 1985). Recent exploration in Western Cape has brought two new species to light both of which can unambiguously be placed in *Brownanthus*.

***Brownanthus fraternus* Klak, sp. nov.**, a *B. corallino* foliis minus papillosis manifeste, seminibus grandioribus cum tumore hilari differt.

TYPE.—Western Cape, 3420 (Bredasdorp): west of Swellendam, (–AA), *Klak 171* (BOL, holo.; K).

Dwarf shrub, decumbent to erect, 150–400 mm high, 500 mm wide. *Branches* articulated, green, succulent, becoming woody with age towards bases; internodes cylindrical, 2.5–8.0 × 3.5–4.0 mm, epidermal bladder cells xeromorphic, ± isodiametric (Figure 1C). *Leaves* deciduous, up to 9 mm long, flattened above, convex below, free towards bases, with mesomorphic epidermal bladder cells without hair-like extensions (Figure 1G). *Calyx* with 5 lobes; lobes shortly connate and erect during anthesis. *Flowers* solitary, borne at tip of stem, 24 mm diam. *Staminodes*: petaloid staminodes white to cream-coloured, free to bases, recurving over calyx lobes; filamentous staminodes absent. *Ovary* semi-inferior; placentation axile. *Fruit* a hygrochastic capsule, 5-locular, 5–7 mm diam., valve wings inflexed over expanded valves, seed bags absent. *Seeds* dark brown, D-shaped, 1.4–1.5 mm long, without crest, testa with raised central papillae, with hilar bulge (Figure 1H). *Flowering time*: December.

Distribution and ecology: Bredasdorp and Swellendam Districts (Figure 2); on quartz patches overlaying clay or on gravelly shale slopes; winter rainfall up to 400 mm.

Specimens examined

WESTERN CAPE.—3419 (Caledon): 10 km north of Napier, (–BD), *Bruyns 6844* (BOL), *Klak 275* (NBG); 2 km north of Napier, (–BD), *Bruyns & Klak 7807* (K). 3420 (Bredasdorp): west of Swellendam, (–AA), *Klak 171* (BOL, holo.; K).

The habit, floral morphology and, in particular, the epidermal features of the stem of *B. fraternus* (Figure

1C) are very similar to those of *B. corallinus* (Thunb.) Ihlenf. & Bittrich (Figure 1B), but the former may be distinguished by its less papillate leaves (Figure 1G). The most conspicuous difference lies in the seeds where there is a hilar bulge in *B. fraternus* (Figure 1H), which is absent in *B. corallinus*.

B. fraternus is known from three localities between Swellendam and Bredasdorp, where it appears to be under threat from agricultural activities. This is much further south than any other *Brownanthus* and it is the only species of *Brownanthus* which grows on the coastal plains south of the Langeberg. The nearest locality of its closest relative, *B. corallinus*, is over 300 km to the northwest at the southern end of Namaqualand. The widespread, but less closely related *B. ciliatus*, is found no nearer than 100 km away from *B. fraternus*.

***Brownanthus glareicola* Klak, sp. nov.**, a *B. corallino* habitu parviore compaciore, pagina caulium hirta, foliis minus papillosis manifeste supra concavis infra convexis foliis junioribus imbricatis, seminibus cristatis distinguenda est.

TYPE.—Western Cape, 3118 (Vanhynsdorp): southwest of Vanhynsdorp, (–DA), *Klak 457* (BOL, holo.; K).

Dwarf, erect shrub up to 170 mm high, 250 mm wide. *Stems* articulated, green, succulent, becoming slightly woody with age towards bases; internodes cylindrical, 3.5–5.5 × 3.5–4.5 mm, epidermal bladder cells xeromorphic with hair-like extensions (Figure 1A). *Leaves* deciduous, up to 3–5 mm long, concave above, convex below, overlapping at bases, epidermal bladder cells mesomorphic without hair-like extensions (Figure 1E). *Calyx* with 5 lobes; lobes shortly connate and erect

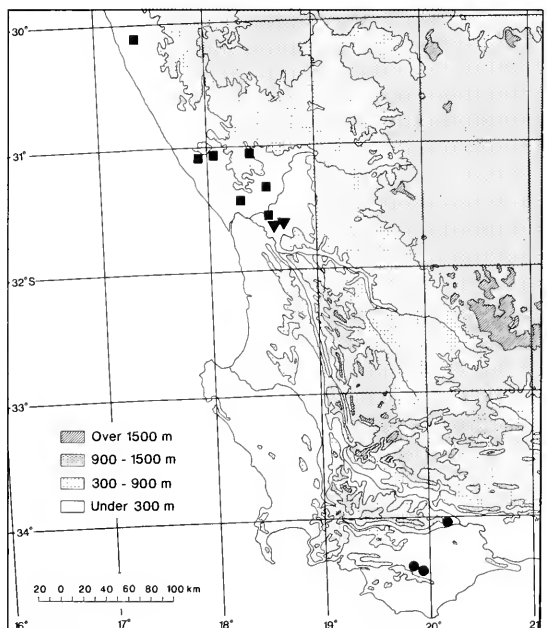


FIGURE 2.—Distribution of *Brownanthus glareicola*, ▴; *B. corallinus*, ■; *B. fraternus*, ●.

during anthesis. *Flowers* solitary at tips of stems, 10–15 mm diam. *Staminodes*: petaloid staminodes white to cream-coloured, free to bases, recurving over calyx lobes; filamentous staminodes absent. *Ovary* semi-inferior; placentation axile. *Fruit* a hygrochastic capsule, 5-locular, (4–)5–6 mm diam., valve wings inflexed over expanded valves, without seed bags. *Seeds* brown, D-shaped, 1.3–1.5 mm long, with a crest, hilar bulge absent, testa cells slightly raised (Figure 1D). *Flowering time*: October.

Distribution and ecology: Knersvlakte, southwest of Vanrhynsdorp (Figure 2); flat to gently sloping patches of quartz gravel on clay; winter rainfall, 100–200 mm per year.

Etymology: *glareicola* = gravel dweller.

Specimens examined

WESTERN CAPE.—3118 (Vanrhynsdorp): southwest of Vanrhynsdorp, (–DA), *Klak 457* (BOL, holo.; K); gypsum mine, (–DA), *Klak 458* (BOL).

The material upon which the description is based, comes from a locality south of Vanrhynsdorp, where the plants were first noticed by A. Ellis and P. Desmet in 1996. The species had previously been misidentified as *Brownanthus corallinus* and grows together with it in one of the known localities. The new species is distinctly smaller and more compact in growth than *B. corallinus* and the older stems are only slightly woody towards their bases. It also differs from *B. corallinus* (Figure 1B) by the hair-like epidermal cells which cover the stems (Figure 1A). Furthermore, the bladder cell idioblasts of the leaves are noticeably more reduced in size compared to the ones in *B. corallinus* and the bases of young leaves overlap, which is never found in *B. corallinus* (Figure 1E, F). In addition, the leaves in *B. corallinus* are sub-cylindrical, whereas in *B. glareicola* they are convex below and concave above. Further differences may be found in the seeds. These have a conspicuous crest in *B. glareicola*, which is not known for any other species of *Brownanthus* (Figure 1D).

Whereas *B. corallinus* is known from numerous localities over a distance of about 250 km in Namaqualand, *B. glareicola* appears to be much rarer and is known from only two localities in the southern Knersvlakte (Figure 2). In all of these it grows on patches of flat to gently sloping quartz gravel.

Erepsia N.E.Br.

Erepsia was revised by Liede (1989). Characteristics separating it from the closely allied genus *Lampranthus* N.E.Br., are the triquetrous leaves with tough epidermis and the presence of a hypanthium. Liede (1989) subdivided the genus into four sections, three of which share flowers with vertical hypanthium walls and leaves usually less than 5 mm diam. The remaining section, *Crassifoliae*, consists of seven species in which the walls of the hypanthium are sloped outwards and the leaves are mostly fairly thick (5–10 mm diam.).

Recently, plants of the very rare *Lampranthus dunensis* were rediscovered on the Cape Flats. This species was described as *Mesembryanthemum dunense* by Sonder (1862). In Jacobsen (1960), L. Bolus moved it to *Lampranthus* and placed it in the informal section *Reptantes*.

An examination of the flowers of this material showed that they differ from those found in all species of *Lampranthus*, in that they possess a conspicuous, outwardly sloped hypanthium. In addition, the broad, triquetrous leaves with tough epidermis are typical of species placed in *Erepsia* section *Crassifoliae*. This feature, together with the noticeable triquetrous leaves suggest that *L. dunensis* belongs in *Erepsia*. The leaves are 4–6 mm broad and fall within the limits included by Liede in Sect. *Crassifoliae*. It is now transferred to *Erepsia*.

Erepsia dunensis (Sond.) Klak, comb. nov.

Mesembryanthemum dunense Sond., *Flora capensis* 2 : 411 (1862). *Lampranthus dunensis* (Sond.) L.Bolus in Jacobsen: 1197 (1960). Syntypes: Western Cape, seashore near Cape Town, *Ecklon s.n.*, *Pappe s.n.* (TCD, lecto., here designated; S).

Mesembryanthemum macrocalyx Kensis: 153 (1909). Type: Western Cape, Skurfpkop near Somerset West, Nov. 1907, *Pillans 1423* (BOL, holo.).

Specimens examined

WESTERN CAPE.—3418 (Cape Town): Sandvlei, (–AB), *L. Bolus 18590* (BOL); Klipfontein Road, (–AB), *Maytham s.n.* (BOL); north-west of Fish Hoek, (–AB), *Pillans 3626* (BOL); Zeekoevlei, (–AB), *Starke s.n.* (BOL); Wolfgat Nature Reserve, (–BB), *Klak 453* (BOL).

Hammeria P.M.Burgoyne

Hammeria was recently established for two species from the Ceres Karoo. The type of the genus is *Hammeria salteri* (L.Bolus) P.M.Burgoyne, with *Ruschia salteri* L.Bolus as its basionym (Burgoyne *et al.* 1998). Even more recently Hartmann (1998b) published a new name, *Lampranthus tanquanus* H.E.K.Hartmann, based on the same type, without reference to the earlier publication of Burgoyne *et al.* (1998).

The absence of closing bodies and the presence of valve wings were the reasons for excluding *Ruschia salteri* from *Ruschia*. Burgoyne *et al.* (1998) suggested morphological similarities to *Antimima*, *Cheiridopsis* and *Chasmatophyllum*, but were unable to place *R. salteri* into any of the existing genera. Hartmann (1998b) noted correctly that the fruits resembled those of the *Titanopsis* type, with thin, flexible, covering membranes bending down into the empty locules, and almost complete covering membranes. In addition, the locules are shallow, so that the lower part of the capsule is bowl-shaped. In contrast, fruits of *Lampranthus* are always deep, \pm funnel-shaped, with firm, complete covering membranes and often additional closing devices below the covering membranes. It is therefore not possible for this species to remain in *Lampranthus*. From the capsule morphology, it appears more likely that closer relationships may be found with species placed in the *Titanopsis* or the *Stomatium* group. A closer study of this complex is needed before it can be decided whether *Hammeria*

may be included in one of the existing genera or indeed deserves generic status.

However, it has so far been overlooked that the same species was named several times by L. Bolus. Since one of these names predates *R. salteri*, a new combination and synonymy are necessary.

***Hammeria meleagris* (L.Bolus) Klak, comb. nov.**

Mesembryanthemum meleagris L.Bolus, in Notes on Mesembryanthemum and allied genera, part 2: 17 (1928). *Lampranthus meleagris* (L.Bolus) L.Bolus: 169 (1939). Type: South Africa, Western Cape, Ceres Div., near Karooport, Sept. 1928, *Pillans 6130* (BOL, holo.!).

Lampranthus longisepalus L.Bolus: 169 (1939). *Mesembryanthemum longisepalum* L.Bolus: 198 (1930). Type: Western Cape, between Karooport and Calvinia, Jan. 1930, *Leipoldt BOL19135* (BOL, holo.!).

Ruschia salteri L.Bolus: 371 (1932b). *Hammeria salteri* (L.Bolus) P.M.Burgoyne et al.: 206 (1998). *Lampranthus tanquanus* H.E.K. Hartmann: 70 (1998b). Type: South Africa, Western Cape, beyond Karooport near the road to Sutherland, 3 Aug. 1932, *Salter 2668* (BOL, lecto.).

Lampranthus stoloniferus L.Bolus: 307 (1965). Type: South Africa, Western Cape, Sutherland Div., 55 miles east of Karooport, June 1965, *F.J. Stayner KG214/65* (BOL, holo.!).

***Scopelogena* L.Bolus**

Mesembryanthemum verruculatum was already known to Linnaeus and had been introduced to England in the early 1730's (Dillenius 1732). L. Bolus later placed this species in *Lampranthus* (Bolus 1950). The plant, however, could be separated from *Lampranthus* by the apparent lack of valve wings and the fact that the capsules do not close completely once they have opened. On the other hand it differs from *Ruschia* by the absence of closing bodies and by the yellow colour of the petals. These reasons prompted L. Bolus to establish a new genus, *Scopelogena*, in 1962 for this species. At the same time she described a second species of *Scopelogena*, *S. gracilis* L.Bolus (1962).

S. verruculata is known only from the Cape Peninsula, whereas *S. gracilis* was described from Grootvadersbosch, east of Swellendam. The latter was said to differ from *S. verruculata* by the more slender, sometimes obtusely keeled, often laterally compressed leaves, with the capsule obconical inside and not angled. Newly collected material from west and south of Swellendam has shown that none of these characters consistently separate *S. verruculata* from *S. gracilis* and that they are conspecific. *S. verruculata* is distributed from Cape Town sporadically eastwards to Herbertsdale, usually occurring on exposed, locally arid, sandstone outcrops.

These investigations have also shown that, contrary to previous descriptions (Bolus 1962), newly ripened capsules which were opened for the first time possessed very narrow, 'seam-like' valve wings. In most of the old capsules this character is no longer visible and this might explain the fact that it was not mentioned in previous descriptions.

Recent exploration has brought to light a second species, which occurs further north of the distribution area of *S. verruculata*. This is now described. Despite the large size of the plant, this species has so far been overlooked by most collectors. It is named after P.V. Bruyns, who was the first to notice it in Namaqualand in 1992.

***Scopelogena bruynsii* Klak, sp. nov., a *S. verruculata* floribus parvioribus luteis ad roseis salmoneisve, praesentia staminodiorum filamentosorum, fructibus repete claudentibus discedit.**

TYPE.—South Africa, Western Cape, Namaqualand, 3118 (Vanrhynsdorp): 10 km north of Nuwerus, (–AB), *Klak & Bruyns 462*, (BOL, holo.; K).

Woody shrub up to 0.3 m high, 1 m wide, with stout, erect or spreading grey to brown stems. *Leaves* crowded, shortly connate, incurved, erect, 3-angled to cylindrical, up to 45 × 5–8 mm, bluntish, shortly mucronate, soft, whitish grey to slightly reddish. *Calyx* with 5 subequal lobes. *Flowers* in much-branched inflorescence; pedicels 4–11 mm long; bracts up to 15 × 11 mm. *Staminodes*: petaloid staminodes in 1 series; filamentous staminodes present, conically collected, papillate at bases; yellow, salmon or pale pink. *Stamens* erect, outer stamens papillate up to middle; anthers yellow; filaments same colour as staminodes. *Nectaries* in crenulate ring. *Ovary* semi-inferior; stigmas filiform, shorter than tallest stamens; placentation parietal. *Fruit* a hygrochastic capsule, ochre, relatively soft and not woody, 5-locular, 3.0–4.5 mm diam., top convex, lower part deep, funnel-shaped, with very narrow valve wings when young, covering membranes present, almost completely covering locules, with fine ridge below covering membrane, expanding keels diverging, without closing body. *Seeds* dark brown, obovate, tuberculate, 1.0–1.1 mm long. *Flowering time*: September and October.

Distribution and ecology: Namaqualand to Clanwilliam and Ceres Karoo (Figure 3); on low, sandstone cliffs; in areas receiving winter rainfall of 100–200 mm.

Specimens examined

NORTHERN CAPE.—3018 (Kamiesberg): near Leeukuil, (–DC), *Bruyns 5267a* (BOL).

WESTERN CAPE.—3118 (Vanrhynsdorp): 10 km north of Nuwerus, (–AB), *Klak & Bruyns 462*, (BOL, holo.; K); Matsikamma, (–DB), *Helm 1656* (BOL). 3119 (Calvinia): Soutpan, (–CD), *Klak 568* (BOL). 3219 (Wuppertal): Dassielloof, (–BA), *Klak 424* (BOL); south of Elandsvlei, (–DA), *Klak 565* (BOL), *Van Jaarsveld 13579* (BOL).

***Scopelogena verruculata* (L.) L.Bolus** in Journal of South African Botany 28: 9 (1962).

Mesembryanthemum verruculatum L.: 486 (1753). *Lampranthus verruculatus* (L.) L.Bolus: 385 (1950). *Ruschia verruculata* (L.) G.D.Rowley: 9 (1978). Iconotype: Dill., Hort. Eltham. t. 203, fig. 259 (1732).

Scopelogena gracilis L.Bolus: 10 (1962). *Ruschia scopelogena* G.D.Rowley: 9 (1978). Type: Western Cape, Grootvadersbos, Dec. 1958, *H. Hall 1506* (BOL, holo.!).

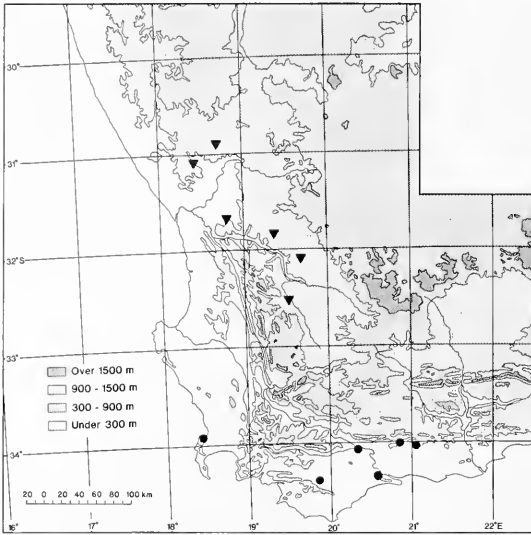


FIGURE 3.—Distribution of *Scopelogenia verruculata*, ●, and *Scopelogenia bruynsii*, ▼.

Woody shrub up to 0.3 m high, 2 m wide, with stout, erect or spreading, grey to brown stems. *Leaves* crowded, shortly connate, incurved, erect, 3-angled to cylindrical, obtuse, up to 16–50 × 3–5 mm, shortly mucronate, very soft, grass green to grey or sometimes reddish. *Calyx* of 5 subequal lobes. *Flowers* in much-branched inflorescence; pedicels 4–15 mm long; bracts up to 15 × 15 mm. *Staminodes*: petaloid staminodes in 1 or 2 series, yellow rarely white; no filamentous staminodes observed. *Stamens* erect, outer stamens dorsally papillate up to middle, inner ventrally papillate at middle; anthers and filaments yellow. *Nectaries* in crenulate ring. *Ovary* semi-inferior; stigmas filiform, longer than stamens; placentation parietal. *Fruit* a hygrochastic capsule, not fully closing again once opened, ochre, relatively soft, not woody, 5-locular, 5–9 mm diam., top convex, lower part deep, funnel-shaped, with very narrow valve wings when young, covering membranes incomplete to almost complete, with inconspicuous ridge below covering membrane, expanding keels diverging, without closing body. *Seeds* dark brown, obovate, tuberculate, 1.1–1.2 mm long. *Flowering time*: September–October.

Distribution and ecology: Cape Peninsula to Riversdale (Figure 3); on sandstone cliffs, with winter rainfall of 300–600 mm annually.

Specimens examined

WESTERN CAPE.—3318 (Cape Town): rocks west of Lion's Head, (–CD), *Hall s.n.* (BOL); Table Mountain, (–CD), *Klak 318* (BOL), *Marloth 2851* (BOL); Lion's Head, (–CD), *Wolley Dod 2420* (BOL). 3419 (Caledon): 10 km N of Napier, Karsrivier, (–BD), *Klak 278* (BOL). 3420 (Bredasdorp): 7 km W of Swellendam, (–AB), *Klak 177* (BOL); Grootvadersbos, (–BB), *Hall 1506* (BOL); Boskloof, Potberg, (–BC), *Burgers 1627* (NBG). 3421 (Riversdale): Glen Leith, (–AA), *Muir 4320* (BOL).

S. verruculata and *S. bruynsii* are morphologically very similar and there appears to be no doubt that this new species belongs in *Scopelogenia*. This is despite the

fact that in the new species the capsules open and close repeatedly. Consequently one of the main distinctions of *Scopelogenia* (that the capsules remain open) falls away. Similar variability in this feature is also found in species of *Aridaria* (Gerbaulet 1996). The flowers of *S. bruynsii* may be yellow, pink or salmon-pink. *S. verruculata* has predominantly yellow or rarely white flowers.

S. bruynsii is found over a wide area, from Nuwerus to Clanwilliam and eastwards to the Ceres Karoo. The plants are always found growing on low sandstone cliffs.

The character combinations present in *Scopelogenia* do not suggest clear affinities to any other genus in the Ruschiodeae and, consequently the relationships of *Scopelogenia* need further study.

The correct identity of *Mesembryanthemum purpureostylum* L.Bolus

In recent literature, much confusion has arisen over the correct identity of *Mesembryanthemum purpureostylum* L.Bolus. The type was based on a collection from Bonnievale. L. Bolus later included this name in the synonymy of *Ruschia forficata* (L.) L.Bolus. Bruyns (1997) was the first to notice that in fact two different species were involved: *R. forficata* (L.) L.Bolus was found to be a synonym of *Erepisia forficata* (L.) Schwantes. Based on the presence of closing bodies and the absence of valve wings, Bruyns (1997) transferred *M. purpureostylum* to *Ruschia*, but, shortly afterwards, it was moved to *Acrodon* by Burgoyne (1998). In the same year, Hartmann (1998b) published a new combination in *Cerochlamys* based on the type of *M. purpureostylum* L.Bolus, however, without reference to any of these recent publications.

The absence of a capsule on the type poses some difficulties for the correct position of this species. However, a watercolour painting of the type specimen exists in the Bolus Herbarium (by M. Page) and this shows the habit, as well as the leaves and flowers. From this it is obvious that the flowers have their filamentous staminodes and stamens collected into a central cone, with the filamentous staminodes overtopping the stamens and partly concealing them. This arrangement is found in numerous other genera such as *Ruschia* and *Antimima*, but in none of the other species of *Cerochlamys*. In *Cerochlamys* the filamentous staminodes are loosely arranged in a cylinder around the stamens, sometimes with the outer ones spreading horizontally (Hartmann 1998b: 51, t. 16, 18, 20). The flower of *Acrodon purpureostylum* shown by Burgoyne matches that of the type. Hartmann, on the other hand, makes no mention of this typical cone flower.

In addition, Hartmann did not find any closing bodies in the capsules of the two collections which she cited. Both Bruyns and Burgoyne mention the presence of closing bodies in their collections. Both Bruyns' and Burgoyne's collections agree with the illustration of the type in all details of habit, leaves and flowers. It can therefore only be deduced that Hartmann must have based her conclusions on misidentified material.

From the characteristics found to be typical of *Acrodon* (Hartmann 1996), Burgoyne (1998) showed conclusively that the species should be placed in *Acrodon* and no reasons have been put forward to alter this. A complete list of synonyms is given below.

***Acrodon purpureostylus* (L.Bolus) P.M.Burgoyne** in *Aloe* 35: 60 (1998).

Mesembryanthemum purpureostylum L.Bolus: 6 (1920). *Erepsia purpureostyla* (L.Bolus) Schwantes: 68 (1928b). *Ruschia purpureostyla* (L.Bolus) P.V.Bruyns: 41 (1997). *Cerochlamys purpureostyla* (L.Bolus) H.E.K.Hartmann: 56 (1998b). Type: South Africa, Bonnievale, Mathews sub NBG3426/15, sheet 2 (BOL., lecto., here designated).

The identity of *Ruschia polita* L.Bolus

Until now much uncertainty has existed about the identity of *Ruschia polita* L.Bolus, which was described in 1932. The type specimen was collected by G. Nel at Touws River in April 1930. Bolus was uncertain whether this species belonged in *Ruschia*, as she placed a question mark next to the genus in her text. The absence of fruits on the type sheet may have added to the confusion. Annotations on the type sheet suggest that it belongs either in *Corpuscularia* or *Antimima*.

However, species placed in *Corpuscularia* are characterised by a peculiar epidermis, which is made up of tightly packed, dome-shaped epidermal bladder-cells. The surface of *R. polita*, on the other hand, consists of flattened cells and is completely smooth. In addition, species of *Corpuscularia* have so far only been recorded from a fairly small area around Port Elizabeth, in the Eastern Cape. Thus, the difference in epidermal morphology and the very disjunct distribution would suggest that the type specimen of *Ruschia polita* is unlikely to belong to *Corpuscularia*.

Exclusion of this species from *Antimima* and *Ruschia* is more difficult since the type lacks any fruits. Nevertheless, since Bolus did not mention the clustering of filamentous staminodes into a dense cone, it seems unlikely that it is either a species of *Antimima* or of *Ruschia*.

A notable feature of the type specimen is, however, its sharply keeled, thick leaves with cartilaginous margins. This is typical of species placed in *Braunsia*. The description of *Braunsia geminata* matches very closely that of *Ruschia polita*, both with respect to the morphology of the leaves as well as the flowers. In addition, the distribution of *B. geminata* extends from the Ceres Karoo to Prince Albert and the Little Karoo and so the type locality of *R. polita* falls within this area. Thus it is reasonable to conclude that *R. polita* is conspecific with *B. geminata*.

***Braunsia geminata* (Haw.) L.Bolus** in *Journal of South African Botany* 33: 306 (1967).

Ruschia polita L.Bolus: 332 (1932a); L.Bolus: 260 (1954). Type: Laingsburg Dist.; Touw's River, Apr. 1930, G. Nel SUG9095 (BOL., holo.).

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Notes on African plants

VARIOUS AUTHORS

AGAVACEAE

AGAVE VIVIPARA: A NATURALISED ALIEN IN SOUTHERN AFRICA

'...invasive species are a kind of habitat destruction. When invasive species take over a habitat, they erase the native richness and diversity of species. What we really need is an everyday concern among ordinary people about biodiversity and the issue of invasiveness.'

—Dr Vandana Shiva in conversation with IUCN's Ricardo Bayon (1997–1998)

The indigenous succulent flora of southern Africa represents 55 mostly unrelated plant families and includes all possible types of life forms. A small minority of exotic succulents (24 species according to Smith *et al.* 1997) can be regarded as naturalised in southern Africa. These species are mostly representative of the Cactaceae (19 species) and, to a much lesser degree, the Basellaceae (1 species), Agavaceae (2 species) and Portulacaceae (2 species) (Smith *et al.* 1997). Some of the species of Cactaceae, e.g. *Opuntia ficus-indica* (L.) Mill. (prickly pear) and *O. aurantiaca* Lindl. (jointed cactus) are aggressive noxious weeds that have invaded and transformed certain parts of the southern African landscape.

In recent years, at least among urban gardeners, the popularity of agavaceous taxa is seemingly on the increase. The plants are being used as inexpensive, permanent barriers to ward off intruders. With their formidable spines, large and compact habit, drought resistance and aggressive growing capability, they are ideally suited for this purpose. With the abandonment of habitations, these hardy agaves can persist without human intervention and subsequently become adventive aliens (Kloot 1987) in the local flora. One such species, *Agave decipiens* Baker was recently recorded in South Africa (Smith & Steyn 1999a). This paper deals with a comparable alien, namely *A. vivipara* L. var. *vivipara*.

Agave vivipara, often known by one of its synonyms, *A. angustifolia* Haw., is a variable species native to central America (Gentry 1982; Forster 1992). It is thought that the species was the wild ancestor of henequén (*A. fourcroydes* Lem.), a cultivated species known worldwide for the high quality of its fibres (Colunga-GarcíaMarín & May-Pat 1993; Colunga-GarcíaMarín *et al.* 1999). Mr Bernard Ulrich (Pforzheim, Germany) has in turn suggested to the second author that *A. vivipara* is possibly a selected form of the widely cultivated *A. sisalana* Perrine, source of sisal hemp. Currently, six varieties, including the typical variety, and two cultivars are recognised in *A. vivipara* (Forster 1992). According to Gentry (1982), this species complex has the most wide-ranging distribution of agaves in North America (for a list of exsiccatae see Gentry 1982: 586–590). The plants commonly occur in tropical savanna, thorn forest and drought-deciduous tropical forests. However, the species also survives in extreme habitats such as the arid Sonoran Desert with about 250 mm rain per annum and in montane pine-oak forests with a yearly precipitation of

1 680 mm. In these natural habitats, wild populations of *A. vivipara* exhibit a gradient in morphological variation, with characters such as plant size, length of leaves, distribution of marginal teeth and mass of leaf fibres showing a high degree of plasticity. Also, improved growth conditions in gardens result in an increase in leaf length and fibre content and a decrease in thorniness (Colunga-GarcíaMarín & May-Pat 1997).

Since pre-Hispanic times, wild populations of *A. vivipara* have been prized by the inhabitants of central America not only for their fibres—which are used for hammocks, bags and fabrics—but also, the peduncles, leaves, stems and roots are used for building material, utensils, tools, food, fermented beverages and medicine (Cruz-Ramos *et al.* 1985; Colunga-GarcíaMarín & May-Pat 1993; Nobel 1994). With increasing attention being paid to the utilisation of invasive aliens (Zimmermann & Zimmermann 1987; Anon. 1988; Howell & Schnell 1991; Turksvykwekersvereniging 1997), southern African environmentalists should take cognisance of the Mexican ethnobotanical uses of *A. vivipara* with a view to duplicating some of these practices locally.

The typical variety of *A. vivipara* is easy to distinguish from *A. decipiens*, the only species with which it can be confused in southern Africa. Important morphological distinctions between the two taxa are given below (Table 1).

TABLE 1.—Main morphological distinctions between *Agave decipiens* and *A. vivipara*

Character	<i>Agave decipiens</i>	<i>Agave vivipara</i>
Habit	Lax rosette crowned by young leaves; stem distinctly thickened by broad leaf bases	Compact rosette with very short internodes; stem not perceptibly thickened by leaf bases
Leaves	Mature leaves laxly disposed horizontally and downward, firm in texture, not very fibrous, leaf blades concave above, convex below, cymbiform in transverse section	Mature leaves radiating, ascending to descending, hard-fleshy, massively fibrous, leaf blades flat in transverse section
Leaf margin	Sinuously toothed	Straight
Marginal teeth	Small, 1–2 mm long, straight to decurved, on low green prominences, firmly attached to leaf margin	Large, up to 5 mm long, with broad bases and slender, decurved (hooked) cusps, easily detachable
Inflorescence	Umbellate branches gracefully upcurved	Umbellate branches spreading horizontally
Flowers	Emitting a strong, fetid scent	Scented, but not foul-smelling

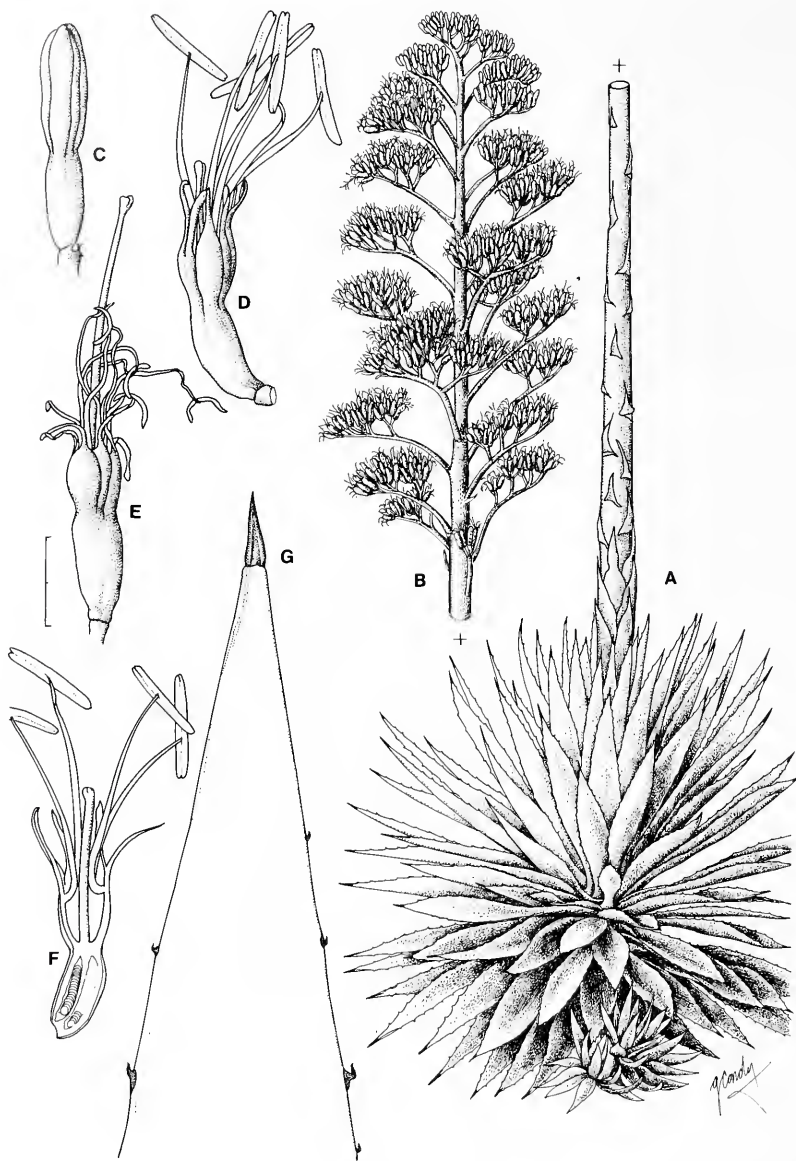


FIGURE 1.—*Agave vivipara* var. *vivipara*: A, habit, rosette 1.5 m tall; B, panicle 2 m tall. C–F, protandrous flower: C, bud; D, male phase; E, female phase; F, longitudinal section. G, distal part of leaf showing straight margin and hooked teeth. C–G, $\times 0.65$. Scale bar: 20 mm. All drawings made from live material collected by E.M.A. Steyn and deposited under G.F. Smith & E.M.A. Steyn 2 (PRE). Artist: G. Condy.

Agave vivipara var. *vivipara* is widely cultivated in Australia and is listed as an established alien in the *Flora of Australia* (Forster 1996). In South Africa this variety, as well as the attractive *A. vivipara* cv. *Marginata* with its yellow-edged leaves, is frequently cultivated (Smith & Steyn 1999b). In urban Pretoria the typical variety has recently been found as a garden escape in a few locations, for example on an open stand (Smith & Steyn 1999b) where the plants had possibly spread from garden refuse dumped earlier, and along a roadside in eastern Pretoria. In the latter location the colony was freely suckering and spreading onto the broad shoulder of the road. Some of the suckering plants were in flower and bulbils were found on an older inflorescence which bore no fruit (Figures 1 & 2A). However, a dried-out infructescence with numerous seed-filled capsules on a dead plant in the same colony showed that the plants are also capable of sexual reproduction (Figure 2B). During germination tests conducted by the first author, $\pm 80\%$ of the large,

black seeds were viable. Similar patterns of distribution and establishment of the species have been observed near Cape Town and Port Elizabeth and Uitenhage, Eastern Cape (Figure 3). *A. vivipara* var. *vivipara* has therefore apparently progressed beyond the adventive stage of naturalisation in South Africa and is currently becoming an established alien (Kloot 1987) like *A. americana* L. and *A. sisalana* (Smith & Mössmer 1996) in the local flora.

1219000-00014 *Agave vivipara* L. var. *vivipara*, Species plantarum 1: 323 (1753). Type: Commelin, Prae-ludia botanica 65, t. 15 (1703) [lectotypified by Wijnands (1983)].

Agave angustifolia Haw. var. *angustifolia*: 72 (1812); Gentry: 559 (1982); Serna & Lopez-Ferrari: 9 (1993); Colunga-Marin & May-Pat: 1455 (1997). Type: St. Helena Island, cultivated. [Neotype: Tozzetti: 2, t. 6 (1810), designated by Gentry: 560, t. 20.6 (1982)].

A. pacifica Trel. in Standley: 118 (1920). Type: Sinaloa, Isla Creston cerca de Mazatlán, Trelease s.n. (MO).



FIGURE 2.—Parts of older inflorescences of *Agave vivipara* var. *vivipara*: A, developing bulbils, $\times 0.9$; B, seeding capsule, $\times 0.9$. Scale bar: 20 mm. Material collected by E.M.A. Steyn and deposited under G.F. Smith & E.M.A. Steyn 2 (PRE). Artist: G. Condy.

A. yaquiana Trel. in Standley: 120 (1920). Type: Sonora, from rocky hillsides between Hermosillo & Ures, *Trelease* 391 (MO).

A. owenii I.M.Johnst.: 999, 1000 (1924). Type: Sonora, on an islet in Guaymas Harbor, *Johnston* 3085 (CAS).

(For a more complete list of synonyms, see Serna & López-Ferrari: 9 (1993).

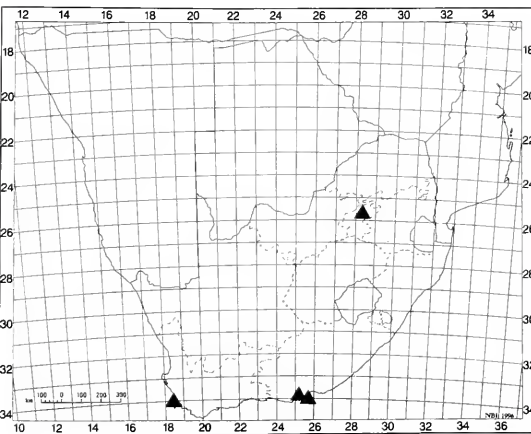


FIGURE 3.—Distribution of *Agave vivipara* var. *vivipara* in southern Africa.

Surculose, caulescent, succulent perennial with radiating rosettes ± 1.5 m diam.; trunk up to 1 m. *Leaves* light green, margins straight, surfaces smooth, hard-fleshy, very fibrous, rigidly spreading, ascending to descending, 0.75–0.9 m long, ± 90 mm wide at midblade, lanceolate, flat in transverse section, narrowed and thickened towards the base; leaf bases broadened, overlapping, stem claspings; teeth easily detachable, usually prominent with low, broad bases and slender cusps, 2–3 mm long, evenly spaced, strongly decurved (apparently releasing an allergen causing painful local swellings when puncturing the skin), commonly reddish brown to dark brown, interstitial teeth usually absent; terminal spine 20–25 mm long, decurrent, conical, reddish brown to dark brown, greying with age, pungent. *Inflorescence* paniculate, 3.5–4.0 m long, bulbiferous after flowering; shaft as long as or slightly longer than panicle; umbels varying in number from 24–36; branches horizontally spreading. *Flowers* yellowish green, about 55 mm long, short-stalked, scented. *Perianth* with tepals unequal, cucullate and pubescent at tip, margins involute, 21–22 mm long, outer segments overlapping the inner; inner segments prominently keeled, wilting before flower reaches female phase, crimping outward and downward; perianth tube succulent, cup-shaped, 11 mm diam. at level of filament insertion, 12 mm deep. *Stamens* exerted 20 mm beyond tepals in male phase flower, yellowish with brownish red speckles; filaments stout, tapered towards apex, inserted in single series in throat of perianth tube, 45 mm long; anthers 22 mm long before dehiscence, cylindrical, yellowish with conspicuous brownish red speckles, versatile. *Ovary* small, 25 \times 10 mm diam., cylindrical, terete, indistinctly grooved in distal region; neck short, slightly constricted; style stout, terete, 72 mm long, light green with brownish red speckles. *Fruit* large, broadly ellipsoid, 30–35 \times 20–25 mm, short-beaked, freely seeding. *Seeds* large, 7–12 \times 6–8 mm, dull black, flattened, D-shaped with complete marginal wing, hilar notch shallow. *Chromosome number* unknown. *Flowering time*: February and March.

GAUTENG.—2528 (Pretoria): Meyers Park area; along Simon Vermooten Road, 0.9 km north of entrance to German School on western shoulder of road, (–CB), G.F. Smith & E.M.A. Steyn 2 (PRE).

Illustrations: Gentry: t. 20.6–20.9 (1982); Smith & Steyn: t. 1 (1999b); Cruz-Ramos et al.: t.1, 2 (1985).

Common names: *kleingaringboom* (Afrikaans). Wild populations in the Yucatan (Mexico) are referred to as *chelem* (Colunga-GarcíaMarín & May-Pat 1997).

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HYACINTHACEAE

CORRECTION OF A HISTORICAL ERROR IN THE TAXONOMIC DESCRIPTION OF *URGINEA CILIATA*

INTRODUCTION

The current interpretation of *Urginea ciliata* (L.f.) Baker is complicated by an unexplained error in Baker's (1875) description of the species. Despite having seen the Thunberg type specimen (*UPS-THUN8281*), Baker clearly states that the distinct cilia on the leaf margins are black. However, on examination of the type specimen, we found that the cilia are hyaline and not black. This was confirmed by herbarium specimens and living plants in the field and in cultivation. The type description is further inadequate due to the absence of a bulb on the specimen and the incorrect assumption that the two leaves preserved on the specimen represent the entire plant. Subsequent treatments (Schönland 1919; Fourcade 1941; Jessop 1977) place the species in *nomina dubia* and result in confusion in herbaria with *Urginea marginata* (Thunb.) Baker.

MATERIALS AND METHODS

The present taxonomic correction is based on a study of herbarium specimens of *Urginea ciliata* and related taxa from relevant herbaria (BOL, GRA, NBG, PRE), of living plants in the field and in cultivation and of archival records housed in the Museum of Evolution, Uppsala University. Representative specimens were compared with a JEOL-JSM 840 scanning electron microscope. Particular attention was paid to the diagnostic cilia found on the leaf margins.

Urginea ciliata (L.f.) Baker in Journal of the Linnean Society 13: 218 (1875); Baker: 464 (1897); Schönland: 41 (1919); Fourc.: 103 (1941); Jessop: 315

(1977). Type: Caput Bonae Spei, Thunberg s.n. (*UPS-THUN8281*, holo.).

Ornithogalum ciliatum L.f.: 199 (1782); Thunb.: 62 (1794); Willd.: 117 (1799); Roem. & Schult.: 528 (1817–1819); Thunb.: 316 (1823); Kunth: 359 (1843).

Plant (100–)250(–300) mm tall. *Bulb* globose, slightly flattened at top, hypogeal, 20–25 mm diam., white turning greenish at apex, scales thick, fleshy, tightly packed; outer tunic transparent on bulb, becoming loose at apices, pale brown, dry, leathery, not neck-forming. *Leaves* 10, the lower six in two whorls of three, ovate, (20–)25(–30) × (15–)17(–19) mm, the upper four in two opposite pairs, three being ovate elliptic, (15–)20(–25) × (7–)10(–15) mm and the uppermost lorate (8–)15(–20) × (3–)4(–5) mm, dark glossy green, firm, leathery, surface smooth, margins densely ciliate, hysteroanthous, prostrate (Figure 4). Desiccated leaves persistent during flowering and dormancy period, brownish, transparent, leathery, marginal cilia obvious (Figure 5). *Inflorescence* erect, 200–260 mm tall, racemose; peduncle and inflorescence axis slender, 1.0–1.5 mm thick, thickest at base, maroon, glossy; fertile part (25–)30–35(–60) × (15–)20 mm with 10–15 flowers; sterile tuft minute, 1 mm long, held at an angle away from the peduncle axis; bracts deltoid, cupped, acute, held at 45° below pedicel, green tinged purplish, 1 × 0.5 mm, basal spur dark purple, 0.5 mm long, apex acute, facing downwards (Figure 6A). *Flowers* scentless; pedicels held at 90° to peduncle in bud, 45° at anthesis and 20° after anthesis, (4–)6 × 0.4 mm, 4–5 mm apart, reddish brown; buds pendulous; perianth patent at anthesis becoming erect after pollination, 12 mm diam., translucent white with light brown keels becoming pale towards apices; lobes spreading,



FIGURE 4.—Leaf arrangement of *Urginea ciliata*, Dold 2383. Scale bar: 10 mm.

equal in length, recurved on either side of keel, fused at base by 0.4 mm, apices with minute stalked papillae, inner lobes broadly ovate with obtuse apices, 5.6×2.6 mm, outer lobes ovate with acute apices, 5.6×1.9 mm (Figure 6B). *Stamens* spreading; filaments white, 3 mm long; anthers bilobed, 1×0.2 mm, green, basifixed. *Ovary* obovoid, 2×1.5 mm, tri-locular, yellow-green; style tubular, longitudinally grooved into three sections, 2 mm long, receptive surface glossy, not swollen. *Capsule* ovoid, erect, $3-7 \times 2.5-5.0$ mm, papery, pale yellow green turning brown (Figure 6C). *Seed* irregularly pyramidal, $2.0-2.5 \times 2$ mm at base, black, shiny, winged; wings thin, papery; testa reticulate.

Urginea ciliata and *U. marginata* specimens are often confused in herbaria as a result of Baker's incorrect and inadequate type description. Complicating matters fur-

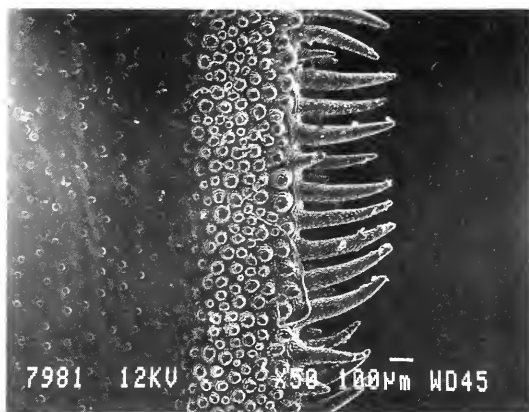


FIGURE 5.—Marginal cilia of *Urginea ciliata*, Dold 2383. Scale bar: 100 µm.

ther, Baker (1875) describes the leaf margin of *U. marginata* as obscurely ciliated, however on examination of the type specimen (*UPS-THUNB8393*), herbarium specimens (BOL, GRA, NBG, PRE) and living specimens we observe that the leaf margin is without cilia at all but is minutely verrucose. The two species are easily distinguished by means of the hyaline marginal cilia present on short rigid prostrate leaves of the latter and the thick cartilaginous margins on spreading to erect leaves of the former. In addition *U. ciliata* has a racemose inflorescence with basifixed anthers while *U. marginata* has an umbellate inflorescence and dorsifixed anthers.

Flowering period is from January to February. Flowers open in pairs in the late afternoon and close before dark—they do not open again. The vegetative growing period is from February to October thereafter dormant to January. The plant is leafless at anthesis with basal leaves reappearing at the time of fruit development or soon afterwards. Thunberg's type sheet is a mixed gathering representing both leaves and inflorescence. Although the bulbs are hypogeal, the well preserved but

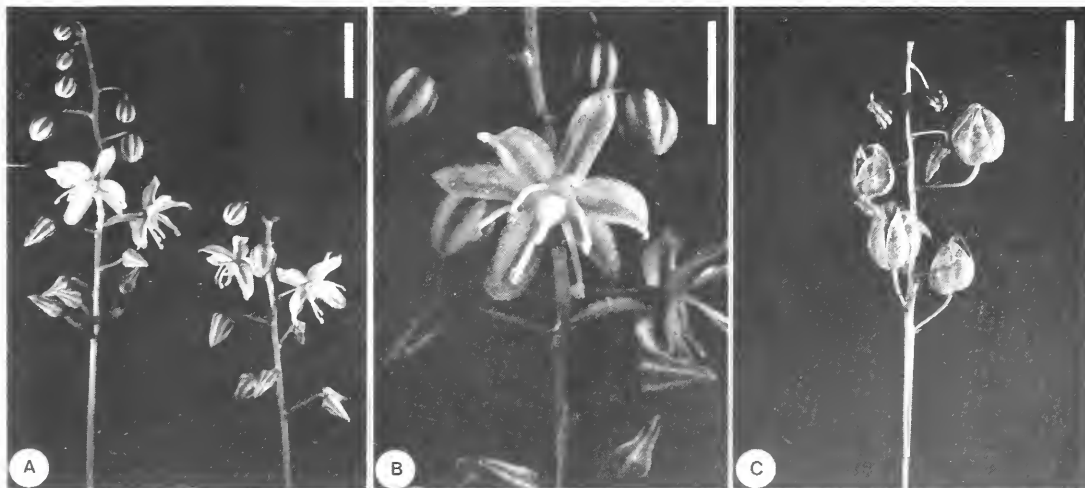


FIGURE 6.—*Urginea ciliata*, Dold 2383. A, inflorescence, B, perianth, C, capsules. Scale bars: A, C, 10 mm, B, 5 mm.

desiccated leaves are persistent and the diagnostic cilia can be seen on specimens collected over the dormant period, enabling identification.

Distribution and habitat

Urginea ciliata is essentially an Eastern Cape species with the majority of collections from the Port Elizabeth and Joubertina Districts. One isolated record from Riversdale reflects a disjunction in distribution (Figure 7). This may be a result of sporadic collections due to its cryptic habit and localised habitat. *U. ciliata* appears to be uncommon and restricted to low grassy fynbos where it is often associated with quartzite outcrops of the Table Mountain Group (Cape Supergroup Peninsula Formation). Populations of up to 40 plants are densely congested between rocks in very shallow sand and gravel soils and are extremely localised. Altitudes from 110 m to 670 m have been recorded.

It has been established that there can be no question as to the validity of the Thunberg type material, as the younger Linnaeus had access to the Thunberg herbarium and he and Thunberg worked in close collaboration on his material in Uppsala (*fide* UPS-THUNB archival records). Furthermore, there is no material of *Ornithogalum ciliatum* L.f. in the Linnaeus herbarium that may have resulted in a mistaken type designation. It is clearly Baker's error, although it is not known why it was caused.

Baker repeated the error of his earlier type description in *Flora capensis* (1897) and applied it as a diagnostic key character. *U. ciliata* was subsequently interpreted as having only two leaves with black cilia on the margins. As a result later collections were erroneously placed in *U. marginata* or not placed at all. Schönland (1919) attributed to the specimen *Cruden 355* from Redhouse, the manuscript name *U. crudeni* (*ined.*) and placed the specimen in a type cover (GRA herbarium practice). He does, however, note that the specimen is closely allied to *U. ciliata*, but was probably misled by Baker's description.

In 1927, Marloth received a specimen from Riversdale, *Muir 4126*, with a note from the collector suggesting that it may be a new species of *Urginea* closely related to *U. ciliata*, but there is no indication of Marloth's opinion. Jessop (1977) discussed *Cruden 355* and *Muir 4126* under *Drimia marginata* (Thunb.) Jessop, *comb. nov.* and remarked that the specimens differ from that species by virtue of the ciliate margins. He was undecided as to the status of the two specimens. He referred to *Ornithogalum ciliatum* L.f. and *Urginea ciliata* under *nomina dubia* despite having seen the Thunberg type (*UPS-THUNB8281*).

Vouchers: *Cruden 355* (GRA, PRE); *Dold 2383* (GRA, UPS); *Fourcade 2930* (BOL), *3569* (BOL); *Muir 4126* (PRE).

Specimens examined

WESTERN CAPE.—3421 (Riversdale): flats around Riversdale, (–AB), *Muir 4126* (PRE).

EASTERN CAPE.—3323 (Willowmore): rocky hills north of Joubertina, (–DD), *Fourcade 2930* (BOL); Wagenbooms River at Joubertina, (–DD), *Fourcade 3569* (BOL), 3324 (Steytlerville): between

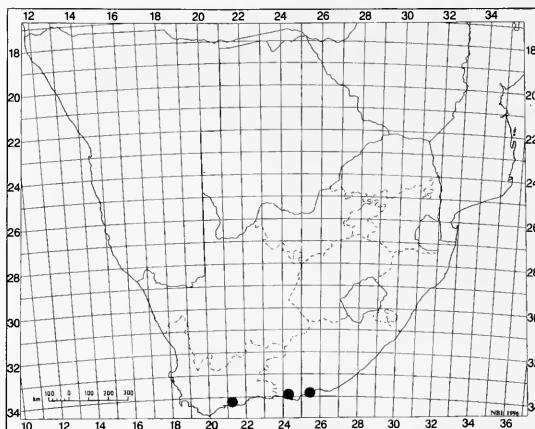


FIGURE 7.—Known distribution of *Urginea ciliata*.

Kareedouw and Assegai Bosch, (–CD), *Fourcade s.n.* (BOL). 3325 (Port Elizabeth): flats around Baakens River Valley, (–DC), *Cruden 355* (GRA, PRE), *Paterson 976*. (GRA); Bridgmead, Parsons Vlei, (–DC), *Dold 2383* (GRA, UPS), *Olivier 3489b* (GRA), *Yates 400* (GRA).

Without precise locality: *Caput Bonae Spei*, *Thunberg s.n.* (UPS).

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ERICACEAE

TWO NEW SPECIES OF *ERICA* FROM WESTERN CAPE, SOUTH AFRICA

Erica orthiocola E.G.H.Oliv., sp. nov. (§*Melastemon*), inflorescentibus floribus duobus in ramulis brevissimis et in synflorescentibus densis aggregatis, corolla breviter infundibuliformi, sepalis pedicello base adnatis, antheris muticis projectione apicale, foliis ciliatis pilis brevibus validis plumosis distinguitur.

TYPE.—Western Cape, 3419 (Caledon): Rivier-sonderend Mtns, Pilaarkop, ridge WNW of peak, 1 540 m, (–BB), 26-02-1999, E.G.H. & I.M. Oliver 11230 (NBG, holo.; K, NY, PRE).

Compact rounded woody shrub ± 300 –(400) \times 300 mm, single-stemmed reseeder. *Branches*: numerous main and secondary with continuous apical growth; internodes short, less than leaf length, no infrafoliar ridges, puberulous with simple spreading to reflexed white hairs. *Leaves* 3-nate, erect to spreading, imbricate, $\pm 5.5 \times 1.5$ mm, oblong-elliptic, adaxially flattened, abaxially rounded, hard and stiff, glabrous, margins with short stubby plumose hairs, apex shortly cuspidate, sulcus narrow and closed at base; petiole 1 mm long, appressed, adaxially glabrous, abaxially puberulous. *Inflorescence*: flowers 2(1) terminal on highly reduced lateral branchlets, appearing axillary on main branches, these branchlets with only 2 bract-like prophylls; pedicel 6 mm long, with very short dense substellate hairs, white to pinkish; bract about $\frac{1}{3}$ up pedicel, 1.5×0.5 mm, oblong, very slightly apiculate, white-pink, semitransparent, glabrous, sparsely ciliate, sulcus very small to absent; bracteoles 2, $\frac{2}{3}$ up pedicel, otherwise like bract. *Calyx* 4-lobed, 2.5×2.0 mm, appressed to corolla; lobes slightly fused at base and to apex of pedicel, ovate, apiculate, the outer two slightly overlapping inner two, stout and hard, scarious with semitransparent marginal zone, pink and green, glabrous, margins with short stout plumose hairs and finer simple hairs, sulcus narrow, $\pm \frac{1}{3}$ length of lobe. *Corolla* 4-lobed, 4×3.5 mm, shortly and broadly funnel-shaped, pink turning brownish, glabrous; lobes erect, 1.5 – 2.0×1.5 mm, ovate, subacute, keeled with a dark longitudinal stripe, margins occasionally toothed to slightly erose. *Stamens* 8, free, manifest; filaments 2×0.4 mm, linear-oblong, slightly narrowed at base, straight, glabrous, whitish; anthers dorsifixed near base, bilobed, V-shaped, muticous; thecae 1.5×0.5 mm, oblong with narrowed slightly elongated tip, papillate, medium brown; pore relatively large, $\frac{2}{3}$ length of theca; pollen in tetrads. *Ovary* 4-locular, $\pm 1 \times 1$ mm, broadly ellipsoid to obovoid, slightly emarginate, glabrous, dull pink, with no basal nectaries; ovules 6–10 per locule pendulous from placenta in upper $\frac{2}{3}$; style far exserted, 6 mm long, filiform, glabrous, white to reddish at apex; stigma small narrowly cyathiform, red. *Fruit* a dehiscent capsule, 2×2 mm, valves splitting for $\frac{2}{3}$ their length to angle of 30° , apices not incurved, septa equal on valves and columella. *Seeds* 0.7×0.5 mm, ellipsoid, yellow to dark brown, testa reticulate, with thick radial cell walls, internally slightly wavy, externally \pm straight. Figure 8.

This new species is characterised by the 2-flowered inflorescence borne on very short lateral branchlets

arranged in a rather dense synflorescence near the ends of the branches, the shortly funnel-shaped corolla, sepals fused to the upper end of the pedicel which is covered with short substellate hairs, and the muticous anthers with an apical projection. The leaves are stiff and hard and edged with short stout plumose hairs.

There are several species similar to *E. orthiocola* based on the pedicel being longer than the corolla, the corolla shape, and anther type with extended portion above the pore, but it differs in a number of respects, the main one being the short stout plumose hairs on the margins of the leaf. *E. pillarkopensis*, which is sympatric with *E. orthiocola*, is a large woody shrub to small tree, with the flowers numerous, bright pink and arranged all over the branches, the leaves and sepals hairy with simple short hairs, and the calyx differently shaped and not fused. *E. seriphifolia* and *E. cubica* both have a simple many-flowered inflorescence on the ends of the main branches, the bract axial, long scattered distinctly plumose hairs on the pedicel, the stem with distinct infrafoliar ridges and the leaf margins with a few short simple hairs. They also have a similar fusion of the sepals with the upper portion of the pedicel. *E. obconica* is similar in the mucronate leaf and obconic stigma, but the bract and bracteoles are in a higher position on the pedicel and the inflorescence is simple and terminal on the main branches. *E. roseoloba* has the similar fusion of sepals but differs by the included style and simple hairs on the pedicel.

The flowers of *E. orthiocola* lack nectaries around the base of the ovary and have a slightly expanded stigma. This would indicate that the pollination is probably effected by wind. This could not be confirmed in the field due to the slightly late stage of flowering we encountered when collecting the type material.

The new species is very localised on a single slope in the Rivier-sonderend Mountains just west of Pilaarkop (Figure 9) where it grows on very steep south-facing rock ledges or small outcrops just below the summit ridge, hence the name *orthiocola* (*orthius* = high, lofty; *colus* = inhabiting). Several visits to the area provided only a few scattered small groups of plants, the largest with about five plants, which had escaped the major fire seven years ago. The plants appear to be very slow-growing since no young plants were observed. *Flowering time*: February and March.

This locality is peculiar in having several species of plants confined to the upper south slopes of the ridge. There are several undescribed *Erica* species including the following one, and the unusual and very rare *Lonchostoma esterhuyseniae* Strid (Bruniaceae). This is probably in part due to the habitat conditions which are cool and moist, with an accumulation of cloudy mist from the southeast winds caused by the leeward position of the ridge in relation to the peak of Pilaarkop.

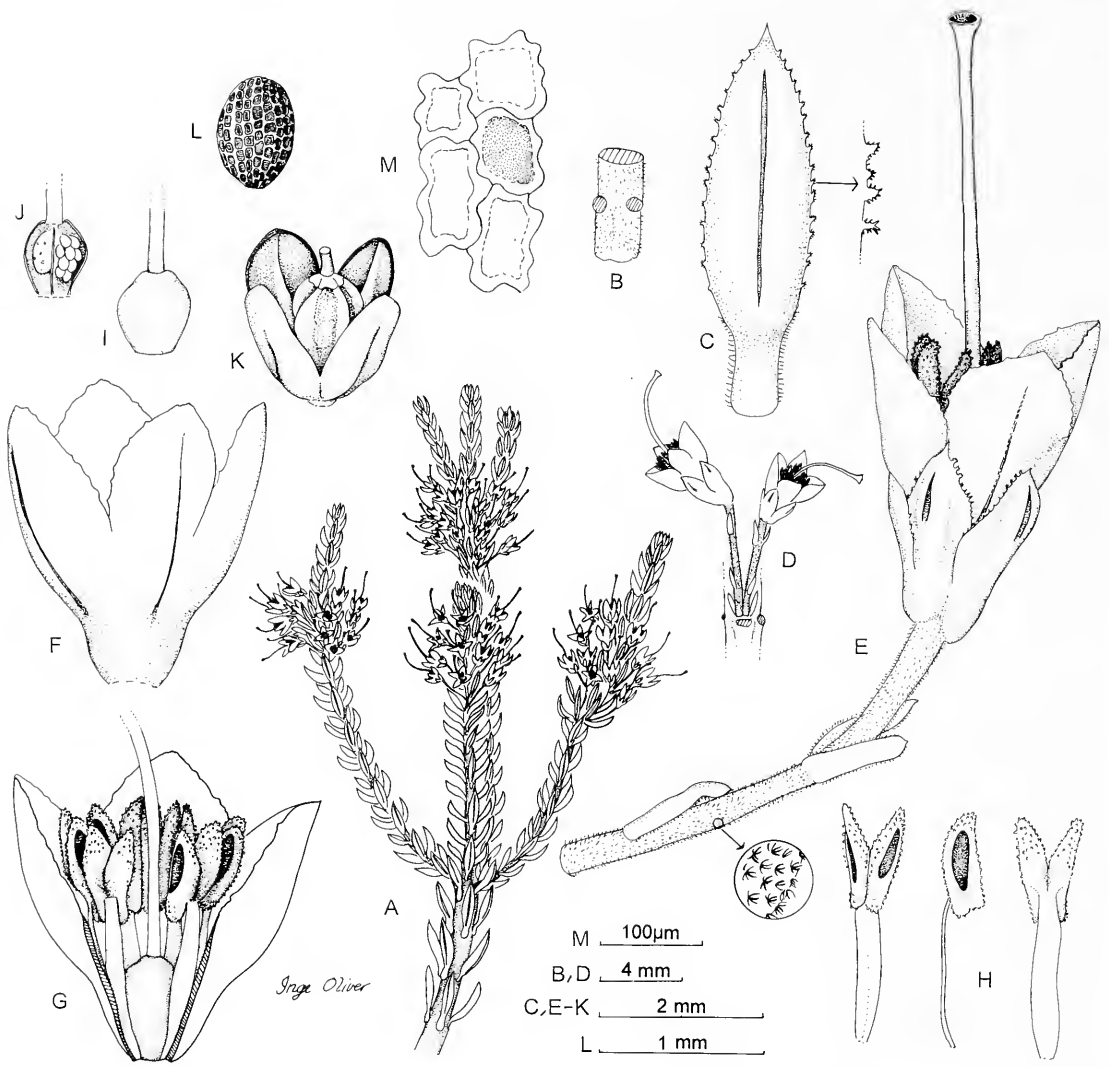


FIGURE 8.—*Erica orthiocola*. A, flowering branch; B, branch; C, leaf; D, inflorescence on very short lateral branchlet with subtending leaf removed; E, flower; F, corolla; G, corolla opened to show androecium; H, stamen, front, side and back views; I, ovary; J, ovary opened laterally; K, capsule; L, seed; M, testa cells. All drawn from the type, *Oliver & Oliver 11230*. A, $\times 1$; B, D, 4 mm; C, E–K, 2 mm; L, 1 mm; M, 100 μ m. Artist: Inge Oliver.

E. pillarkopensis appears to have been very abundant on the southern slopes of the ridges just west and east of Pilaarkop as evidenced by the numerous silvery grey skeletons remaining after the extensive fire in 1994. This is particularly so in the upper portion of the main kloof of Olifantsbosch. At present there are very few old plants of the species remaining and these are only in rocky areas where they escaped the fire. Some are in the region of 3 m high with a trunk of 200 mm diam. Surprisingly there are very few young plants visible on any of the slopes.

E. seriphiifolia, *E. cubica* and *E. obconica* all occur on the Langeberg range with *E. cubica* extending as far away as the South Coast of KwaZulu-Natal. *E. roseoloba* is restricted to a single peak in the Klein Swartberg near Seweweekspoort and was only recently described (Oliver & Oliver 1996).

Paratype material

WESTERN CAPE.—3419 (Caledon); Riviersonderend Mtns, Pilaarkop, 5400 ft, (–BB), 8-03-1970, *Esterhuysen 32416* (BOL); *ibid.*, 4500–4800 ft, 7-03-1971, *Esterhuysen 32579* (BOL, K); *ibid.*, 9-04-1971, *Esterhuysen BOL55092* (BOL); *ibid.*, 1 520m, 9-10-1998, *Oliver 11177* (NBG); *ibid.*, 04-1940, *Stokoe 7877* (BOL); *ibid.*, 06-1949, *Stokoe SAM62327* (BOL, SAM).

***Erica columnaris* E.G.H.Oliv., sp. nov.** (*\$Hermes/Chlorocodon*), synflorescentibus densis columnaribus, foliis floribus superantibus, bracteolis plerumque plene recaulescentibus, calcaribus antherarum brevibus ex parte decurrentibus, nectariis nullis distinguitur.

TYPE.—Western Cape, 3419 (Caledon): Riviersonderend Mtns, Pilaarkop, moist southern slopes below ridge WNW of peak, 1 500 m, (–BB), October 1998,

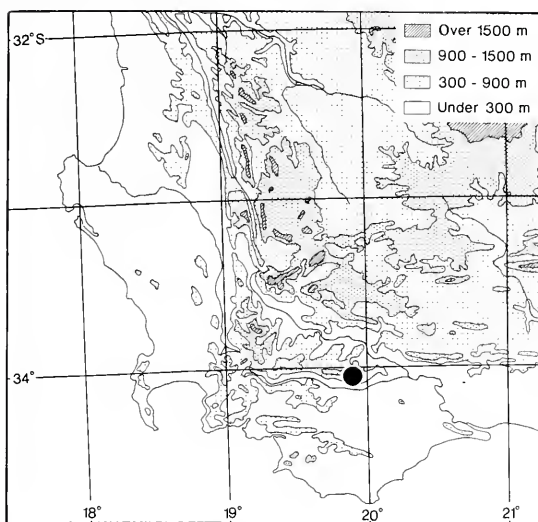


FIGURE 9.—Known distribution of both *Erica columnaris* and *E. orthiocola*.

E.G.H. & I.M. Oliver 11177 (NBG, holo.; BM, BOL, E, K, MO, NY, P, PRE, S, W).

Stoutish, erect, virgate shrub 0.5(–1) m high, single-stemmed reseeder. *Branches*: main branches of previous season often devoid of leaves and terminating in a compact innovation zone of 7–15 fastigiate leafy secondary branches, these terminating in synflorescences 15–40 mm long, branches glabrous with infrafoliar ridges, tertiary branchlets very reduced, 0.5 mm long terminating in a florescence. *Leaves* 4–6-nate, subspreading-incurved, imbricate, 7–8 × 1 mm, lanceolate, flat adaxially and slightly rounded abaxially, glabrous, ciliolate, sulcus narrow and closed at base; those on tertiary reduced branchlets in 2 or 3 whorls, very small, bract-like and whitish; petiole 0.8 mm long, appressed, glabrous, ciliolate. *Inflorescence*: 1(2) flowers subterminally on very reduced lateral branchlets appearing axillary to the longer leaves on secondary branches, these arranged in column-like synflorescences 15–40 mm long at ends of secondary branches; pedicel 2 mm long, glabrous; bract partially recaulescent $\frac{1}{3}$ up the pedicel, 1 × 0.7 mm, ovate, acute, esutate, glabrous, ciliolate, light green; bracteoles 2, fully recaulescent as lateral lobes of calyx, occasionally 2 partially recaulescent and appressed to calyx, rarely in middle position, when partially recaulescent then like the bract in shape. *Calyx* 4-partite; lobes appressed to corolla, occasionally lateral two imbricating at base, 1.5 × 1 mm, ovate-lanceolate, glabrous, ciliolate, green often tinged red, sulcus narrow, $\frac{1}{3}$ length of sepal. *Corolla* 4-lobed, 2.5 × 2.5–3.0 mm, urceolate, glabrous, wine-red with whitish base; lobes recurved, 0.8 × 1 mm, broadly triangular, margins entire. *Stamens* 8, free, included; filaments 1 mm long, broadly oblong, flat, straight in upper half, glabrous, white; anthers bilobed, ovate in front view, awned; thecae erect, appressed, glabrous, dark brown; awns decurrent on filament, \pm 0.1 mm long, linear, simple, pendulous, white; pore $\frac{1}{2}$ length of theca; pollen in tetrads. *Ovary* 4-locular, 8-lobed, 0.5 × 0.8 mm, oblate obovoid, emarginate, glabrous, reddish green, nectaries absent;

ovules 4 per locule, spreading from placenta in central position on columella; style exerted, 2.5 mm long, narrowly cylindric, sometimes slightly curved apically, glabrous, greenish white base and dark red apex; stigma peltate-capitate, sometimes reflexed, dark red. *Fruit* a dehiscent capsule, 1.2 × 2 mm, valves splitting to \pm 45° and nearly to the base, septa \pm 30% and very thin on columella and 70% on valve, placenta very convoluted, columella easily shed from capsule. *Seeds* 0.5 × 0.4 mm, ellipsoid, circular in cross section, yellow brown, testa reticulate, cells 60 × 90 μ m, radial walls narrowly wavy. Figure 10.

This new species is distinguished by the dense compound synflorescence, the leaves of which are longer than the lateral flowers, the bracteoles often fully recaulescent as the lateral segments of the calyx, the short anther spurs which are partially decurrent along the apex of the filament, and the absence of nectaries. The pseudospicate, columnar synflorescences give the species its name, *columnaris* is pillar- or column-like.

Several species show alliances with *E. columnaris* based on the long erect tightly packed synflorescences with small corolline flowers and stems with infrafoliar ridges. *E. regerminans* with a very similar habit and method of branching, differs in its slightly larger, more conspicuous dark pink flowers that are longer than the leaves, its corolla being ellipsoid with a longer pedicel and in the long anther spurs which are not decurrent. *E. dodii* differs in having a soft delicate growth form, corolla more open cyathiform to campanulate, anthers small and delicate with spurs much longer but slightly decurrent, style included, flowers pink not dark purplish pink and larger and more visible. *E. coarctata* Wendl. differs in the flowers being slightly smaller and more cyathiform and greenish cream-coloured sometimes tinged pink, the anthers lacking spurs, the stigma peltate-cyathiform and far exerted, and the ovary not emarginate.

E. columnaris exhibits clearly the transition from partially to fully recaulescent bracteoles in the Ericaceae which condition was noted in the problems with the delimitation of the genera *Philippia* Klotzsch (Oliver 1988) and *Ericinella* Klotzsch (Oliver 1994). In \pm 70% of the flowers, it would appear that the bracteoles have been lost, whereas they have recaulesced fully with the pedicel and become incorporated in the calyx as the apparent lateral sepals. This will be addressed in a forthcoming publication dealing with the relationship of the rest of the minor genera of the Ericaceae to *Erica*.

The lack of nectaries and the expanded stigma complex would indicate that the pollination syndrome for the species is anemophily. On walking through a large dense population, occasional puffs of pollen were noted coming from disturbed plants. However, there were numbers of small beetles visiting the inflorescences of some plants. This could suggest a case of evolutionary change from entomophily to anemophily taking place in a species. We postulate that this is the situation in a number of other species of *Erica*. The occurrence of fully recaulescent bract and bracteoles is always accompanied by loss of nectaries, expansion of the stigma and anemophily in the Ericaceae.

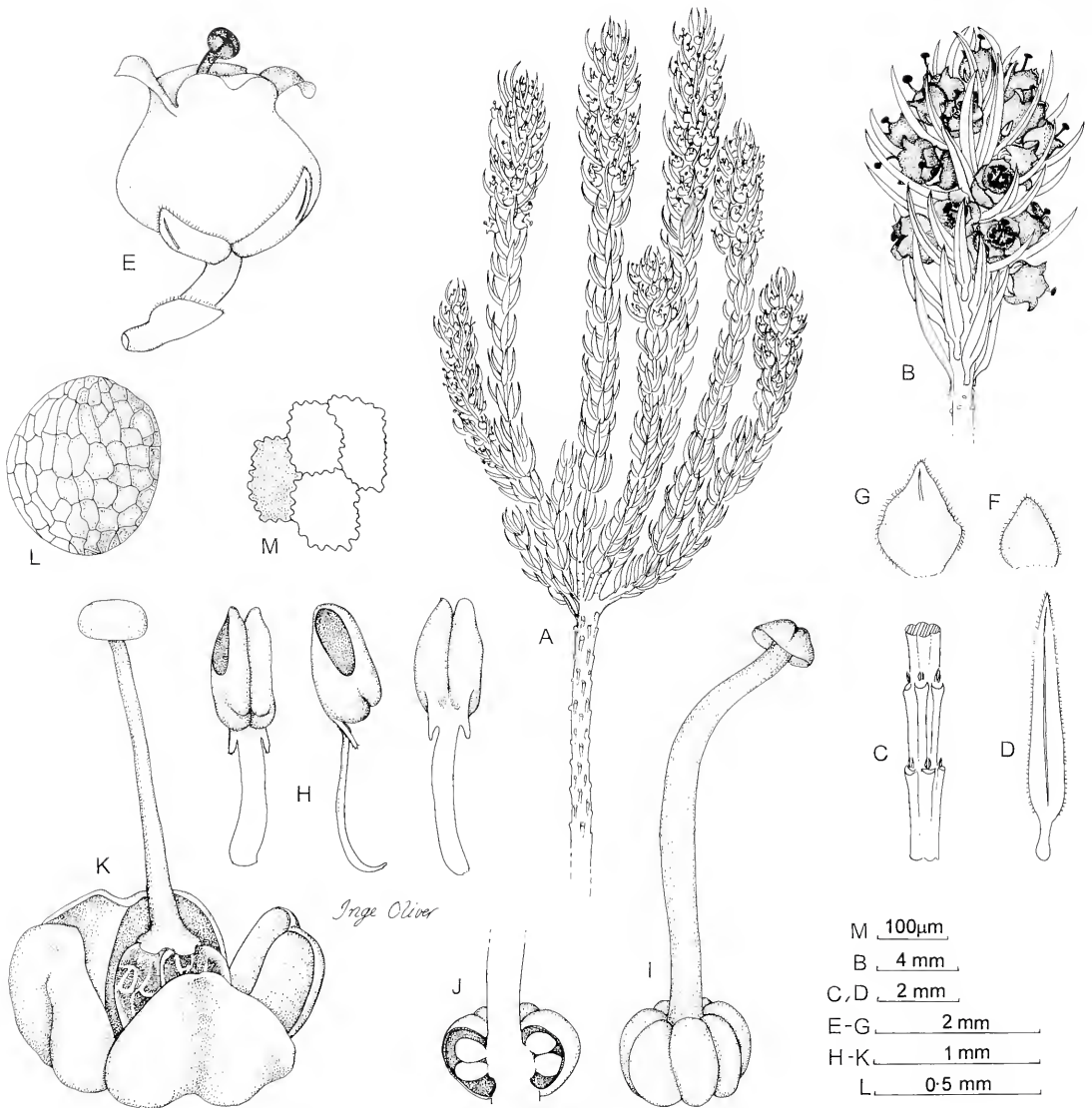


FIGURE 10.—*Erica columnaris*. A, flowering branch; B, flowering branch, close-up; C, stem with leaves removed; D, leaf; E, flower; F, bract; G, sepal; H, stamen, front, side and back views; I, gynoecium; J, ovary opened laterally; K, capsule; L, seed; M, testa cells. A–J, drawn from type, *Oliver & Oliver 11117*; K–M, drawn from *Oliver 10940*. A, $\times 1$; B, 4 mm; C, D, 2 mm; E–G, 2 mm, H–K, 1 mm; L, 0.5 mm. Artist: Inge Oliver.

The new species is confined to the steep southern slopes of the ridge, just west of the main peak of Pilaarkop in the Riviersonderend range (Figure 9), which is the only known locality. It forms dense stands of plants in some areas, mostly on the loamy open slopes away from the rocks inhabited by *E. orthiocola*. Flowering time: September and October.

E. regerinans is confined to moist south-facing slopes in the Langeberg range, whereas *E. coarctata* is widespread from the Cape Peninsula to the George area where it grows on dry lower slopes of sometimes coastal flats associated with calcareous deposits. The latter species has been noted by us to be a resprouter in several well-separated localities.

E. dodii occurs from the Cape Peninsula to the Riviersonderend Mountains where it grows sympatrically with *E. columnaris*, sometimes less than a metre apart, but then up against or under overhangs of large rocks and rock faces with a soft delicate habit no more than 200 mm high.

Paratype material

WESTERN CAPE.—3419 (Caledon): Riviersonderend Mtns near Lindeshof, Pilaarkop, 4000 ft, (–BB), 17-11-1965, fruiting, *Esterhuysen 31400* (BOL, K); *ibid.*, 4500 ft, 24-10-1971, *Esterhuysen 32718* (BOL, NBG, PRE); *ibid.*, 4750 ft, 28-10-1997, fruiting, *Oliver 10940* (K, NBG, NY, PRE).

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ASPHODELACEAE: ALOOIDEAE

THE GENUS *POELLNITZIA* INCLUDED IN *ASTROLOBA*

Considered by various authors to be a species of *Aloe* L., *Astroloba* Uitewaal or *Haworthia* Duv., the monotypic *Poellnitzia rubriflora* (L.Bolus) Uitewaal has had a particularly chequered taxonomic history since its original description in the genus *Apicra* Willd. (Smith 1994). Vegetatively the species shows close affinities to some species of *Astroloba* and accords completely with the genus in its tubular, actinomorphic flowers with included stamens. A close relationship between the two genera is also supported by the results of a preliminary survey of lipophilic anthranoid aglycones in the roots of subfamily Alooideae (B.-E. van Wyk pers. comm.). The genus *Poellnitzia* was distinguished from *Astroloba* on the basis of the red flowers with connivent, reduplicate-valvate tepals (Smith 1995; Smith *et al.* 1995). Careful examination of the flowers, however, shows that the aestivation is in fact imbricate and the species thus differs from *Astroloba* only in the more or less horizontal racemes bearing secund, orange-red flowers with connivent tepals. These floral adaptations are now recognised as part of the syndrome of sunbird pollination which is widespread in southern Africa (Goldblatt & Manning 1999) and the resemblance between the flowers of *Poellnitzia* and the bird-pollinated genus *Microloma* R.Br. (Apocynaceae: Asclepiadoideae) is particularly striking. In the wild the species is visited by Lesser double-collared sunbirds, which insert just the tip of their beak into the flowers before extending the tongue into the tube to extract the nectar. Species of *Astroloba* are pollinated by anthophorine bees and have smaller, dull-coloured flowers. The sugar composition of the nectar of *Poellnitzia* also reflects a shift from insect- to bird-pollination

and is hexose-dominant whereas the nectar of *Astroloba* is sucrose-dominant (Van Wyk *et al.* 1993). Adaptations for specialised pollination strategies alone are insufficient grounds for the recognition of genera and we believe that *Poellnitzia* is best treated as a species of *Astroloba* adapted to pollination by sunbirds.

***Astroloba rubriflora* (L.Bolus) G.F.Sm. & J.C.Manning**, comb. nov.

Apicra rubriflora L.Bolus, The Annals of the Bolus Herbarium 3: 13, t. 2D (1923). Type: South Africa, Western Cape, Bonnievale, Smith *s.n.* (BOL, holo!).

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ALOE DELPHINENSIS IN ALOE SECT. LOMATOPHYLLUM

The genus *Lomatophyllum* Willd. has been distinguished from *Aloe* L. primarily by the former having fleshy, indehiscent fruit (berries) with unwinged seeds and the latter having dehiscent fruit (capsules) with winged seeds. Smith & Van Wyk (1991) following a cladistic analysis of the subfamily Alooideae (Asphodelaceae), concluded that *Lomatophyllum* could be easily included in *Aloe* but that a comprehensive taxonomic revision of the species concerned was required. Evidence from chromosome morphology, leaf surface anatomy, pollen morphology (Schill 1973) and leaf sap flavanoid chemistry (Viljoen *et al.* 1998) all lend support

to this move to reduce *Lomatophyllum* to the synonymy of *Aloe*.

Rowley (1996) has proposed that species included in the genus *Lomatophyllum* be transferred to *Aloe* as members of *Aloe* sect. *Lomatophyllum* G.D.Rowley. Various new combinations and new names have been proposed to validate this proposal (Rowley 1996; Newton & Rowley 1998). These automatic transfers have done little to resolve the species relationships in the group. However, Rauh (1998) has recently provided an identification key to the 18 species he included in his concept of *Lomatophyllum*.

A comprehensive, phylogenetically based, infrageneric classification of *Aloe* is not currently available. Reynolds (1966, 1982) chose to recognise 10 sections in the genus *Aloe* s.s. However, the continued use of his classification has been questioned in recent times on the basis of chemical investigations (Viljoen *et al.* 1998). Van Wyk & Smith (1996) did not mention these sections at all and used informal groups to arrange the South African species of *Aloe*. The recognition of *Lomatophyllum* at sectional rank in *Aloe* is probably not equivalent to that used by Reynolds (1966, 1982) in defining the various sections in the genus. Hence the infrageneric classification of *Aloe* remains to be resolved and a different rank such as subgenus may need to be considered for the taxa of *Lomatophyllum*, assuming monophyly of this infrageneric unit.

Nevertheless the characters used to define the section *Lomatophyllum* are distinctive and easily ascertained if fresh fruit are available. There are a number of species of Madagascan *Aloe* for which the fruit are unknown (cf. Rauh 1995, 1998) and hence their sectional classification is unknown. One of these is *Aloe delphinensis* Rauh (1990), based on his collection *Rauh 68629a* from Pic St. Louis, near Fort Dauphin in southwest Madagascar. Rauh (1990) allied the new species to *A. bakeri* Scott Elliot but subsequently considered that a further new species *A. lucile-allorgeae* Rauh was the closest relative of *A. delphinensis* (Rauh 1998).

Fruit set was stimulated in a cultivated specimen of *Aloe delphinensis* using pollen from *A. dinteri* Berger, a 'true' *Aloe* from Namibia (Reynolds 1982). These fruits were fleshy and indehiscent, and contained wingless seeds (Figure 11).

Aloe delphinensis can be included in *Aloe* sect. *Lomatophyllum* thus bringing the number of included species in that section to nineteen. This species may be distinguished from the other Madagascan taxa in the group by inserting an additional couplet into the key of Rauh (1998).

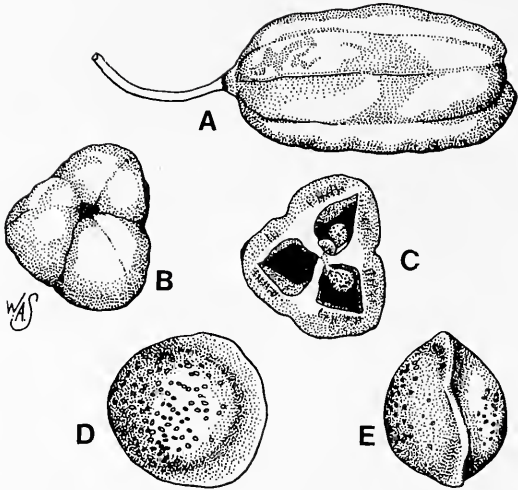


FIGURE 11.—*Aloe delphinensis*. A–C, fruit: A, side view, $\times 2$; B, apical view, $\times 2$; C, cross section, $\times 2$. D, E, seed, $\times 10$. All from fresh material of P.I. Forster PIF24630 [voucher at Queensland Herbarium (BRI)] prepared from a plant purchased by N. Carr in a Madagascan nursery as this species and in close agreement with the protologue and accompanying illustrations of Rauh (1990, 1995, 1998).

***Aloe* L. sect. *Lomatophyllum* G.D.Rowley in**
Excelsa 17: 59 (1996).

***Aloe delphinensis* Rauh** in *Cactus & Succulent Journal* (US) 62: 230 (1990). Type: Madagascar, on granitic rocks on the Pic St. Louis, near Fort Dauphin, 100 m, *Rauh 68629a* (holo., HEID).

Fruiting pedicel 14–15 \times ± 0.5 mm, glabrous. *Fruit* oblong, triquetrous, indehiscent and fleshy, 18–20 \times 9–10 mm diam. *Seed* \pm globose, ± 2 mm diam., with a minute ring or ridge around $\pm \frac{2}{3}$ of the circumference (Figure 11).

Key to Madagascan species

(based mainly on Rauh 1998, but with nomenclature updated for inclusion within *Aloe*)

1a	Plants with bulbils in the inflorescence	2
1b	Plants without bulbils in the inflorescence	3
2a	Rosettes small, with leaves spreading, green with white bands and spots; bulbils 1 or 2, in the floral region	<i>A. propagulifera</i> (Rauh & Raz.) L.E.Newton & G.D.Rowley
2b	Rosettes larger, with leaves erect, uniformly green; bulbils in the axils of bracts up the scape	<i>A. schilliana</i> L.E.Newton & G.D.Rowley
3a	Stems decumbent, short, richly branched, forming dense mats	<i>A. socialis</i> (H.Pcrrier) L.E.Newton & G.D.Rowley
3b	Stems erect, single or branched from the base, but not forming dense mats	4
4a	Plants with thick stems to 100 mm diam. and 2–3 m tall with a large terminal leaf rosette	<i>A. peyrierasii</i> Cremers
4b	Plants with thinner and shorter stems	5
5a	Stems short, to 0.5 m and 10–20 mm in diam.	11
5b	Stemless rosette plants or with very short stems	6
6a	Rosettes small, to 0.5 m in diameter; leaves spreading or erect	7
6b	Rosettes larger, stemless or with a short stem; leaves 0.1–1.0 \times 0.1–0.12 m	8
7a	Leaves narrow linear, erect, densely dentate along the margins; in cultivation forming dense clumps; inflorescence much longer than leaves	<i>A. belavenokensis</i> (Rauh & Gerold) L.E.Newton & G.D.Rowley
7b	Leaves triangular, not densely dentate	9

8a	Leaves up to 1 × 0.1–0.12 m, acute; inflorescences much exceeding the leaves	<i>A. occidentalis</i> (H.Perrier) L.E.Newton & G.D.Rowley
8b	Leaves shorter, with rounded apices; inflorescences shorter than the leaves	<i>A. orientalis</i> (H.Perrier) L.E.Newton & G.D.Rowley
9a	Leaf blades with large deltoid marginal teeth, often chocolate brown; raceme few-flowered, globular	<i>A. prostrata</i> (H.Perrier) L.E.Newton & G.D.Rowley
9b	Leaf blades with small marginal teeth, not chocolate brown; raceme elongated	10
10a	Flowers lemon yellow with green tips	<i>A. citrea</i> (Guillaumin) L.E.Newton & G.D.Rowley
10b	Flowers rose pink	<i>A. rosea</i> (H.Perrier) L.E.Newton & G.D.Rowley
11a	Inflorescences shorter than the leaves	12
11b	Inflorescences longer than the leaves	13
12a	Stems not creeping at the base; leaves very long and narrow, at least over 0.3 m	<i>A. oligophylla</i> Baker
12b	Stems very thin and stolon-like at the base, creeping and producing adventitious roots; leaves shorter, 0.2–0.3 m long	
		<i>A. antsingyensis</i> (Leandri) L.E.Newton & G.D.Rowley
13a	Stems not branching from base, leaf blades green, straight; raceme dense with hanging flowers	
		<i>A. namorokaensis</i> (Rauh) L.E.Newton & G.D.Rowley
13b	Stems branching from base, leaf blades bluish green or brownish green, spirally rolled in upper part or decurved; raceme lax	14
14a	Leaf blades bluish green; marginal teeth 10–15 mm apart; floral tube 25–30 mm long; fruit globose, ± 12 mm diam.	
		<i>A. anivoranensis</i> (Rauh & Hebding) L.E.Newton & G.D.Rowley
14b	Leaf blades brownish green; marginal teeth 2–8 mm apart; floral tube 20–22 mm long; fruit oblong, 9–10 mm diam.	
		<i>A. delphinensis</i> Rauh

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Morphology and anatomy of the rhizome and frond in the African species of *Polystichum* (Pteropsida: Dryopteridaceae)

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Keywords: anatomy, lamina, morphology, *Polystichum*, Pteridophyta, rhizome

ABSTRACT

The generic circumscription of the polystichoid ferns within the Dryopteridaceae and their relationships has been and still is much debated. Although floristic accounts for *Polystichum* are available for many parts of the world, its morphology and evolutionary trends within the genus are still poorly understood. In this study, primarily based on the *Polystichum* species from Africa and neighbouring islands, the morphology and anatomy of the rhizome and frond are addressed. Several species from other genera within the Dryopteridaceae are used for comparison, to gain a better understanding of generic affinities and evolution in this family.

INTRODUCTION

Polystichum Roth is a cosmopolitan genus comprising 180 to 200 species. Although floristic accounts of the genus exist for many parts of the world, a comprehensive modern taxonomic account for the genus as a whole has never been undertaken. The circumscription and definition of species within the genus are still weak. Reasons for the group's inadequate taxonomic status include the occurrence of common and widespread allopolyploid taxa (D.H. Wagner 1979), sterile F1 hybrids, apomictic taxa, substantial phenotypic variation within populations and in most cases, a lack of critical morphological studies.

The morphology and anatomy of *Polystichum* representatives from the Indian subcontinent was studied by Chandra & Nayar (1982) and those of western North America by D.H. Wagner (1979). *Polystichum*, *Arachniodes* Blume, *Cyrtomium* C.Presl, *Dryopteris* Adans. and *Phanerophlebia* C.Presl form a closely related group of genera within the tribe Dryopterideae and are here referred to as the polystichoid ferns. *Cyrtomium* and/or *Phanerophlebia* are often included in *Polystichum* (Tryon & Tryon 1982; Kramer 1990). Yatskievych (1996), however, treated *Cyrtomium* and *Phanerophlebia* as distinct genera and showed that both have a closer affinity with *Polystichum* than with each other, a hypotheses first proposed by Christensen (1930). The genera *Arachniodes*, *Dryopteris* and *Polystichum* are not always clearly separable, as each include species that display characters generally associated with the other genera. The proposed close affinity of these genera is also supported by the occurrence of a natural hybrid between *Dryopteris* and *Polystichum* (W.H. Wagner 1985). Widén *et al.* (1981) showed that phloroglucinols widespread in *Dryopteris* also occur in *Arachniodes* but are rare in *Polystichum*. Indusia, when present, are peltate in *Polystichum* and reniform in *Arachniodes* and

Dryopteris. All these genera, however, also contain species that are exindusiate.

This study is primarily based on *Polystichum* species from Africa, Macaronesia, the Madagascan region and the Marion Island groups, but observations on species from outside of this region are also considered. For comparative purposes several species from other genera within the Dryopterideae were included in the study. The aim is to gain a better understanding of generic affinities within the Dryopterideae and to speculate on possible evolutionary trends within the group.

MATERIALS AND METHODS

Material used in the anatomical study was obtained from the wild and from cultivated plants (Table 1). Voucher specimens are housed at the Compton Herbarium (NBG). Fresh material was fixed in FAA for at least 24 hours. For rhizomes, serial sections were cut by hand, stained with alcian blue for one minute, rinsed in water and temporarily mounted in glycerine. Camera lucida drawings were prepared at $\times 7.5$, $\times 15$ or $\times 31.25$ magnifications using a Wild 'Heerbrugg' microscope. The stelar structure of the rhizome was reconstructed using these sections.

Roots, stipes, rachises, secondary rachises and laminae were sectioned 45 μm thick using a Reichert-Jung Hn 40 freeze microtome. Sections were stained with safranin and alcian blue for one minute, rinsed in water and dehydrated in a series of 50% ETOH, 40% ETOH:60% toluene, 20% ETOH:80% toluene and 100% toluene, after which they were permanently mounted in Entellan (Art. 7961, E. Merck, Darmstadt).

For describing the vasculature of the stipe and lamina fresh material was used; freehand serial sections were made at 2.5 or 5 mm intervals along the entire length of the axis, noting where bundles divide or fuse and where pinnae and pinnules originate.

Epidermal features were studied using pinna or pinnule fragments removed from selected specimens, and

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TABLE 1.—Material examined in the study of the rhizome and frond stelar structure

Taxon	Voucher	Origin
Rhizome		
<i>Arachniodes webbiana</i> (A.Br.) Schelpe subsp. <i>foliosa</i> (C.Chr.) Gibby <i>et al.</i>	Roux 2573	NORTHERN PROVINCE.—2329 (Pietersburg): Louis Trichardt, Hanglip Forest Station, (–BB).
<i>Polystichum</i>		
<i>dracomontanum</i> Schelpe & N.C.Anthony	Roux 2715	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, Tugela Gorge, (–DB).
<i>incongruum</i> J.P.Roux	Roux 2678	EASTERN CAPE.—3227 (Stutterheim): Amabele, (–DA).
<i>incongruum</i> J.P.Roux	Roux 2695	EASTERN CAPE.—3226 (Fort Beaufort): Hogsback Forest Station, (–DB).
<i>incongruum</i> J.P.Roux	Roux 2713	WESTERN CAPE.—3322 (Oudtshoorn): Knysna, Touws River, (–DC).
<i>macleae</i> (Baker) Diels	Roux 2561	MPUMALANGA.—2530 (Lydenburg): Sabie, (–BB).
<i>monticola</i> N.C.Anthony & Schelpe	Roux 2513	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB).
<i>transkeiense</i> W.B.G.Jacobsen	Roux 2540	KWAZULU-NATAL.—2731 (Louwsburg): Ngome Forest Reserve.
<i>transvaalense</i> N.C.Anthony	Roux 2510a	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB).
<i>wilsonii</i> H.Christ	Roux 2521	FREE STATE.—2829 (Harrismith): Harrismith, Platberg, (–AC).
Frond		
<i>Cyrtomium caryotideum</i> (Wall. ex Hook. & Grev.) C.Presl var. <i>micropterum</i> (Kunze) C.Chr.	Roux 501	EASTERN CAPE.—3325 (Port Elizabeth): Settler's Park, (–DC).
<i>Dryopteris</i>		
<i>antarctica</i> (Baker) C.Chr.	Roux 2632	WESTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, (–AC).
<i>athamantica</i> (Kunze) Kuntze	Roux 348	GAUTENG.—2627 (Potchefstroom): Roodepoort, Strubens Valley, (–BB).
<i>dracomontana</i> Schelpe & N.C.Anthony	Roux 2764	LESOTHO.—2928 (Marakabeis): Semonkong, LeBihan, (–CC).
<i>inaequalis</i> (Schltdl.) Kuntze	Roux 1975	EASTERN CAPE.—3129 (Port St Johns): Port St Johns, (–DA).
<i>inaequalis</i> (Schltdl.) Kuntze	Roux 1933	KWAZULU-NATAL.—2831 (Nkandla): Nkandla Forest, (–CA).
<i>pentheri</i> (Krasser) C.Chr.	Roux 1984	EASTERN CAPE.—3227 (Stutterheim): Isidinge Forest, (–CA).
<i>pentheri</i> (Krasser) C.Chr.	Roux 1989	EASTERN CAPE.—3227 (Stutterheim): Evelyn Valley Forest, (–CA).
<i>pentheri</i> (Krasser) C.Chr.	Roux 1892	FREE STATE.—2829 (Harrismith): Farm Metz, (–CA).
<i>Polystichum</i>		
<i>dracomontanum</i> Schelpe & N.C.Anthony	Roux 2715	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB).
<i>incongruum</i> J.P.Roux	Roux 2678	EASTERN CAPE.—3227 (Stutterheim): Amabele, (–DA).
<i>luctuosum</i> (Kunze) T.Moore	Roux 2709	EASTERN CAPE.—3227 (Stutterheim): Pirie Forest, (–CB).
<i>macleae</i> (Baker) Diels	Roux 2548	MPUMALANGA.—2430 (Pilgrim's Rest): Graskop, (–DD).
<i>monticola</i> N.C.Anthony & Schelpe	Roux 2520	KWAZULU-NATAL.—2829 (Harrismith): forest south of Seheletwane, (–AC).
<i>pungens</i> (Kaulf.) C.Presl	Roux 2370	WESTERN CAPE.—3318 (Cape Town): Table Mountain, (–CD).
<i>setiferum</i> (Forssk.) T.Moore ex Woy. n.	<i>Sine coll. s.n.</i>	Madeira.
<i>transkeiense</i> W.B.G.Jacobsen	Roux 2498	EASTERN CAPE.—3029 (Kokstad): Weza Forest, (–DA).
<i>transvaalense</i> N.C.Anthony	Roux 2516	KWAZULU-NATAL.—2829 (Harrismith): forest south of Seheletwane, (–AC).

cleared using household bleach. Once cleared the material was repeatedly rinsed in clean water and semi-permanently mounted in either glycerine or glycerine jelly. Cover slips were sealed with Entellan.

RESULTS AND DISCUSSION

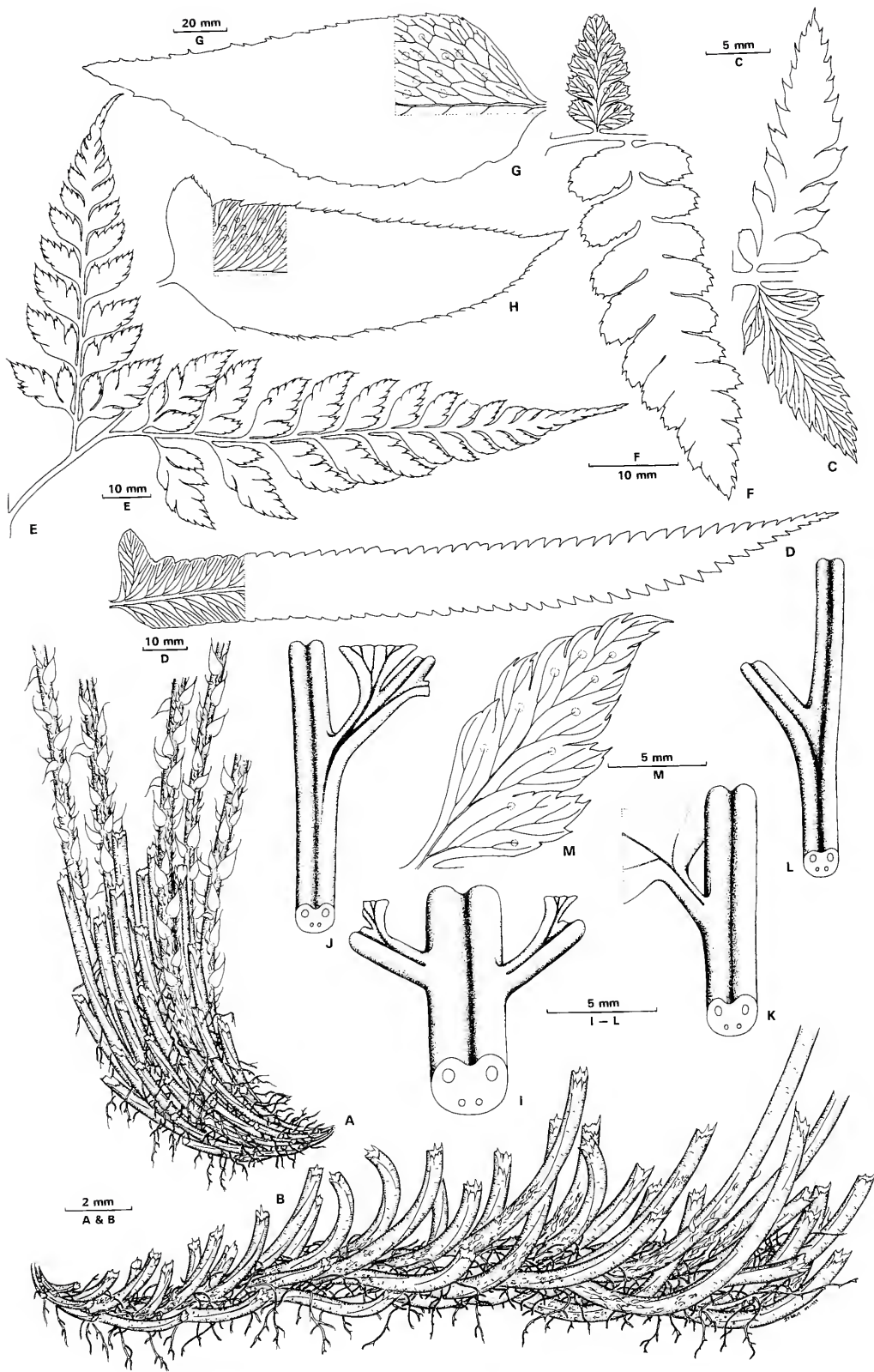
MORPHOLOGY

Rhizome

Detailed studies of the rhizome of *Polystichum* are scant and its morphology remains poorly known. The rhizome anatomy of *Cyrtomium falcatum* was studied by

Gibson *et al.* (1984) and found to be basically identical to that of *Polystichum*. Rhizomes are rarely represented in herbarium collections, hence in modern floristic accounts they are often not mentioned. In many species the rhizome is bulky and this may explain why most collectors are deterred from collecting them. The *Polystichum* species studied by Chandra & Nayar (1982) in India, all have short, stout, and erect rhizomes that are mostly unbranched. In African species two distinct rhizome types, namely, erect and decumbent occur. The erect rhizome type is short and generally unbranched with a large number of fronds crowded in the apical region (Figure 1A). Up to seven leaf gaps overlap at any given time. This rhizome type is sheathed by a mass of wiry roots, with

FIGURE 1.—Rhizome and lamina morphology. A–D, *Polystichum*: A, erect rhizome type in *P. transvaalense*, Roux 2585. B, C, *P. incongruum*: B, decumbent rhizome type, Roux 2377; C, acroscopic proximal pinnules, basicopic pinnule shows free venation, Roux 2385. D, *P. macleae*, Roux 2242, acroscopic pinna, section shows free venation. E, L, M, *Arachniodes webbiana* subsp. *foliosa*, Roux 1001: E, basicopic proximal pinnule; L, rachis section showing confluent nature of axes sulci; M, pinnule segment showing venation. F, *Dryopteris inaequalis*, Taylor 4264, basicopic proximal pinnule and acroscopic pinnule with free venation; G, *Cyrtomium caryotideum* var. *micropterum*, Roux 1913, section of pinna outline with reticulate venation; H, *Phanerophlebia auriculata*, pinna outline with section showing venation, after Yatskievych (1996). I, J, *P. transkeiense*, Roux 2493: I, proximal part of rachis showing non-confluent nature of axes sulci; J, distal part of rachis showing confluent nature of axes sulci; K, *C. falcatum* ex hort., non-confluent nature of sulci. All vouchers housed in NBG. Scale bars: A, B, 2 mm; C, I–M, 5 mm; D–F, 10 mm; G, H, 20 mm.



helically arranged persistent stipe bases several layers deep and, at least in the younger parts, also with paleae, giving greater bulk to the rhizome; the highly dissected stellar structure suggests that it is derived. The decumbent rhizome type is usually long and branched, terete to slightly laterally or dorsoventrally flattened; up to five leaf gaps overlap at a time; the fronds are generally more widely spaced, often exposing the rhizome internodes (Figure 1B). In both rhizome types paleae form a dense covering especially over the apical region.

Branching of the rhizome takes place through the formation of lateral buds at regular or irregular intervals along the main stem. Branching in *Polystichum transkeiense* W.B.G.Jacobsen is regular. In certain habitats, *P. incongruum* J.P.Roux, *P. monticola* N.C.Anthony & Schelpe and *P. pungens* (Kaulf.) C.Presl also show regular branching. In *P. dracomontanum* Schelpe & N.C.Anthony and *P. marionense* Alston & Schelpe, lateral buds initiate the formation of long stoloniferous outgrowths. As a result, large clonal stands are formed by these species. Fronds are initially widely spaced along these stolons but marked primary thickening takes place distally, and the fronds become more closely spaced. Roots are irregularly formed over the entire length of the stolons. Since the thinner stoloniferous branches can rot away more readily, individual rhizomes may become isolated thus serving as a means of clonal propagation.

Branching and stolon formation is here viewed as an adaptation for plants occurring in environments not always conducive to sexual reproduction. Species with this type of rhizome often occur in more exposed, often dryish habitats that may also be subjected to periodic fires. It is therefore also possible that the clonal habit might be an adaptation to periodic burning. The short, suberect to erect rhizome type is, however, much more common in the genus. In contrast to the decumbent rhizome type, the erect rhizome of the African species mostly remains unbranched resulting in these species occurring as individuals rather than as clonal clusters. Plants with this rhizome type are also adapted to a wide range of habitat conditions, but tend to be more site-specific. The erect rhizome is generally well seated in the substrate, whereas the decumbent rhizome type mostly grows epigeally, although the stolons of *P. dracomontanum* are subterranean. Occasionally the rhizome in *P. transkeiense* may also be subterranean.

Species in the genera *Arachniodes*, *Cyrtomium*, *Dryopteris* and *Phanerophlebia* have either erect or decumbent rhizomes. If the cyatheoid ferns are accepted as an ancestor of the dryopteroid ferns, as suggested by Bower (1928); Ching (1940); Copeland (1947); Nayar (1970, 1979) and Holttum (1973), then the short erect rhizome should be viewed as the primitive state and the decumbent rhizome as derived. However, a dennstaedtioid origin as proposed by Holttum (1947) and Pichi Sermolli (1977) would suggest the reverse. Hasebe *et al.* (1995) and Pryer *et al.* (1995) presented strong morphological and molecular evidence that Dennstaedtiaceae branched off the tree below the Dryopteridaceae, with Cyatheaceae considerably below that. The evolutionary transformation of the rhizome habit thus remains open to debate.

Roots

An abundance of wiry adventitious roots occurs irregularly over the entire surface of the rhizome, often forming a dense fibrous mass. Roots appear to be long-lived but they are, however, only initiated at or near the growing apex of the rhizome. Young roots are whitish to pale brown and mostly simple, whereas older roots are dark brown to black and frequently monopodially branched. Golden brown root hairs form a dense covering a short distance behind the root apex. They do, however, lose their function on the older parts of the roots and become abraded. In the erect rhizome type, roots also provide good anchorage.

Fronds

All the *Polystichum* species within the study area are evergreen; the fronds remain alive for at least two annual cycles. The fronds are persistent and are shed through decay or mechanical damage only. A type of frond re-orientation as described by Noodén & W.H. Wagner (1997), occurs in *P. wilsonii* H.Christ. In this high altitude species, which frequently grows in exposed sites, a large percentage of the fronds may collapse during the cold winter months. The plants are, however, never entirely deciduous. Frond length varies considerably among species and in *P. incongruum* it can attain a length of 1.8 m. There is a strong correlation between the rhizome type and the number of fronds borne by a plant. Species with an erect rhizome always bear more fronds than those with a decumbent rhizome. In *P. transvaalense* N.C.Anthony, up to 27 fronds are borne by each plant, whereas in species with a decumbent rhizome, the number of fronds rarely exceeds seven. Fronds in the *Polystichum* species studied are monomorphic, with no evident differentiation between the sterile and fertile fronds. The fronds are differentiated into a distinct stipe and lamina. Vernation of the fronds is initially circinate, but as the stipe and lamina elongate, the juvenile fronds become hook-shaped in species such as *P. dracomontanum*, *P. luctuosum* (Kunze) T.Moore, *P. transvaalense* and *P. wilsonii*. Monomorphic fronds are most common in the Dryopterideae, but in *Dryopteris*, e.g. *D. dracomontanum* Schelpe & N.C.Anthony, they are dimorphic.

Stipe

The use of stipe characters in fern taxonomy has been studied by Lin & De Vol (1977, 1978). They clearly illustrate that stipe characters, especially anatomy, are more useful at the generic and family level than at the species level. The stipe in all the studied species of *Polystichum* is firm. In species with erect rhizomes the stipes grow directly upwards, whereas in species with a decumbent rhizome, they are initially strongly curved upwards. Stipe length and diameter are variable but may be up to 930 mm long in *P. incongruum* and up to 10 mm diam. in *P. volkensii* (Hieron.) C.Ch. In most species the stipe base is variously rounded adaxially and abaxially, but distally they all become shallowly to deeply sulcate adaxially. In most taxa the basal part of the stipe is castaneous (brownish) to ebeneous (black) and often lustrous (nitid), becoming paler distally in dried material. In

live plants, however, the distal part of the stipe generally remains green. The stipe bases of the African *Polystichum* species appear not to be modified into distinct trophopods as described by W.H. Wagner & Johnson (1983). Trophopods have been reported for all the *Phanerophlebia* species with the exception of *P. macrosora* (Baker) Underw. (Yatskievych 1996). In most species the dorsolateral aerophore line is conspicuous throughout the length of the stipe, generally being somewhat paler in colour than the surrounding tissue. In *P. luctuosum* the aerophore line is often green, thus contrasting strongly with the generally castaneous to ebeneous stipe. The stipe is always clothed with paleae, the density of which shows considerable variation amongst the species.

Lamina

Most *Polystichum* species in the study area have 2-pinnate pinnatifid to 3-pinnate laminae, with 1-pinnate laminae recorded in *P. falcinellum* (Sw.) C.Presl, *P. kalambaititense* Tardieu, *P. macleae* (Baker) Diels and *P. maevaranense* Tardieu only. *P. macleae* has laminae ranging from 1-pinnate to 2-pinnate. Lamina length varies considerably between species with the longest laminae, up to 925 mm, having been recorded in *P. volkensii* (Hieron.) C.Ch. Lamina outline also shows variation between species, but within a species the degree of variation is fairly restricted.

Pinnae and pinnules are borne subopposite to alternate on the rachis and secondary rachis. Proximally the pinnae and pinnules are usually short-stalked but distally they become sessile and eventually adnate. They are mostly herbaceous in texture, but in *P. dracomontanum* and *P. marionense*, both of which grow in harsh conditions, the pinnules are usually coriaceous. The lamina is always discolorous with the adaxial surface darker in colour. Adaxially the pinnules are pale to dark green in colour, but in *P. dracomontanum* and *P. incongruum* at Hogsback in the Eastern Cape, exposed and older fronds generally turn bronze.

Polystichum is characterised by a largely acroscopic pinna development (Figure 1C, D), but basiscopically developed laminae are often present in *P. vestitum* (G.Forst.) C.Presl and *P. whiteleggei* Watts. The degree to which the proximal acroscopic pinnules are developed shows considerable inter- and infraspecific variation. Interspecific variation is exemplified especially in *P. drepanum* (Sw.) C.Presl, *P. incongruum* and *P. macleae*.

In *Arachniodes* and *Dryopteris* the laminae are mostly basiscopically developed (Figure 1E, F). In *Arachniodes* and in *Cyrtomium* and *Phanerophlebia*, where most species have 1-pinnate laminae, the pinnae are also acroscopically developed and often conspicuously auricled (Figure 1G, H, M).

In *Polystichum* the pinnae are mostly oblong-acuminate to narrowly oblong-acuminate in outline, but in some species they may be ovate, narrowly triangular, or in *P. marionense* often deltoid. In some species the proximal pinnae are reduced towards the base of the frond,

and often also strongly conduplicate and deflexed. In most species the proximal pinnae are usually widely spaced with no or little overlap with the more distal ones. Towards the lamina apex, however, the pinnae frequently become imbricate. The number of stalked pinnae per lamina ranges from 12 to 15 in *P. maevaranense*, but up to 45 in *P. setiferum* (Forssk.) T.Moore ex Woy. Pinna length in most species falls within the 100 to 200 mm range, but in *P. marionense* the pinnae may reach a maximum length of only 36 mm, whereas in *P. drepanum* the proximal pinnae may be up to 450 mm long.

Pinnules are always inaequilateral, asymmetric and variously ovate, trullate or rhomboid in outline, with an acroscopic auricle. The base is mostly truncate acroscopically whilst basiscopically it is mostly narrowly to broadly cuneate. Margins may be lobate, serrate, doubly serrate or dentate with the teeth being obtuse, pungent or aristate. Pichi Sermolli (1972), in describing *P. kilimanjaricum* Pic.Serm., emphasized the number and direction of the pinnule awns, but we found them to be extremely variable and of no taxonomic value. In *P. marionense* the pinnule margins of plants growing in exposed conditions are often revolute. The number of short-stalked pinnules per pinna ranges from five in *P. marionense* to 27 in *P. zambesiaceum* Schelpe. Pinnules are mostly small, but in *P. drepanum* the proximal acroscopic pinnule can be up to 83×15 mm. Indumenta occur on both the adaxial and abaxial lamina surfaces of most species with the abaxial surface generally more densely set.

Rachis

Chromatically the rachis does not differ significantly from the stipe, being green throughout, but in older fronds it may become dark brown proximally. The aerophore line that extends from the stipe is generally visible with the naked eye and may be paler or darker in colour than the surrounding tissue. The rachis is mostly straight throughout its length but distally it may become slightly flexuose in some species. Adaxially the rachis forms a V-shaped sulcus along its entire length. In *P. luctuosum* the sulcus is shallow and not very prominent. Holttum (1959) stressed the importance of the external shape of the rachis in defining related groups: in the *Dryopteris*-group of ferns, to which *Polystichum* belongs, the rachis has a median sulcus that opens adaxially to admit the sulcus of the secondary rachises; the raised edges of the secondary rachis sulcus join the sides of the costa sulcus with the edge of the pinnule-lamina decurrent on the secondary rachis as a lateral wing.

Our observations on live *Polystichum*, *Cyrtomium* and *Dryopteris* material show that the rachis sulcus does not always open to admit the secondary rachis sulcus, as the pinna stalk is often terete, especially in the lower part of the lamina (Figure 1I, J, K). In *Arachniodes*, however, the sulci of the rachis and that of the lower order axes are confluent (Figure 1L). Paleae similar to those occurring on the stipe extend to the rachis. Palea density on the rachis is, however, determined by the species and to a lesser degree also by the prevailing environmental conditions.

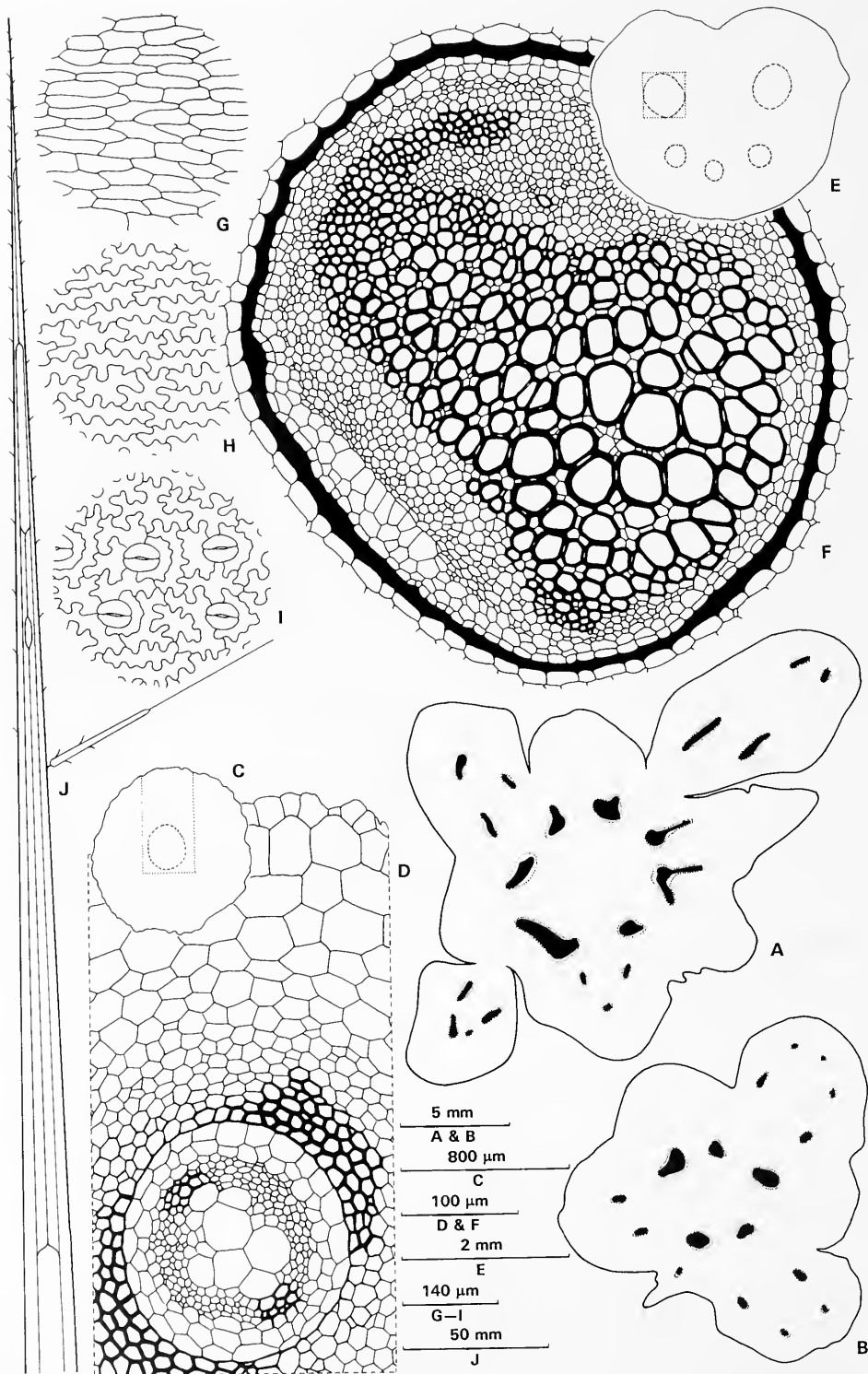


FIGURE 2.—Rhizome, root and frond anatomy in *Polystichum*. A, B, *Polystichum transvaalense*, Roux 2510A (NBG); B, *P. dracomontanum*. C, *Polystichum* root; D, *Polystichum* vascular bundle of rachis. E, *Polystichum* rachis; F, *Polystichum* dorsal vascular bundle of rachis. G, *P. crinulosum*, sine coll. s.n. (P), adaxial epidermis; H, I, *P. aculeatum*, Maire s.n. (RAB), adaxial and abaxial epidermal cells; J, *P. transkeiense*, Roux 2498 (NBG), schematic presentation of frond vasculature showing branching and fusion of vascular bundles along axes. B–D, *Roux 2715* (NBG); E, F, *Roux 2377* (NBG). Scale bars: A, B, 5 mm; C, 800 μm; D, F, 100 μm; E, 2 mm; G–I, 140 μm; J, 50 μm.

Bulbils

Bulbils are here defined as buds or outgrowths capable of developing into an independent plant. Although external stimuli may contribute to the formation of bulbils, this ability largely appears to be fixed genetically. In the polystichoid ferns the ability to produce gemmae appears to be restricted to *Polystichum*, *Dryopteris* and *Phanerophlebia juglandifolia* (Willd.) J.Sm. Within *Polystichum* a diverse group of species is capable of producing bulbils. They have been recorded in sections *Lasiopolystichum* Daigobo, *Metapolystichum* Tagawa, *Macropolystichum* Daigobo, *Cyrtomiopsis* Tagawa, *Stenopolystichum* Daigobo and *Haplopolystichum* Tagawa emend. Daigobo. Bulbils in *Polystichum* are borne either at the retuse apex of a terminal pinna, at the apex of an extended glabrous rachis or, as in the case of the species within the study area, adaxially on the rachis near the frond apex in or near the pinna 'axils'. One to three bulbils per frond appear to be the norm, but in *P. pauciaculeatum* Bonap. up to five bulbils are borne by a frond. Paleated bulbils may also occur near the pinna apices in *P. tsaratananense* Tardieu and occasionally on the stipe of *P. setiferum* (Moore 1855). African and Madagascan species bearing gemmae include *P. crinulosum*, *P. kilimanjaricum*, *P. maevaranense*, *P. magnificum* F.Ballard, *P. pauciaculeatum*, *P. tsaratananense* and *P. volkensii* and total 27% of the species within the defined area. Within the Madagascan region 62% of the species are bulbiliferous compared with the 64% of species occurring in the West Indies (Mickel 1997).

Most taxa which produce bulbils seem to occur in moist or tropical conditions where this form of vegetative reproduction may contribute to more rapid colonisation in areas of fierce competition. Bulbil formation in the ferns, its distribution and ecological implications, requires further study. The fact that bulbil formation occurs in clearly unrelated taxa suggests that it originated independently in these groups.

Venation

Venation patterns in the genera of the Dryopterideae are diverse. This is the principle character commonly used to segregate *Cyrtomium* and *Phanerophlebia* from *Polystichum*. In *Polystichum* the veins of all the species in the study area are always free and anadromous (Figure 1C, D), but in the circumboreal *P. braunii* (Spenn.) Fée, at least some of the veins are catadromous (Kramer 1987). Most veins run into the teeth where they always terminate near the lamina margin. In *P. volkensii* the veins show a slight enlargement towards their apices.

In the fertile pinnules of 2-pinnate species of *Polystichum*, the veins mostly terminate in the soral receptacle midway between the costa and the margin. This feature is also found in several *Arachniodes* and *Dryopteris* species. Variations, however, do occur with the fertile vein often extending for a short distance beyond the sorus. However, in 1-pinnate *Polystichum* and free-veined *Phanerophlebia* species, the venation of the fertile pinnae shows no or little differentiation from that of the sterile pinnae, in that the veins bearing sori are

not conspicuously shortened, thus extending well beyond the sorus (Figure 1H). Also in most *Dryopteris* species the sori-bearing veins are not shortened and extend to the margin (Figure 1F).

Cyrtomium and some *Phanerophlebia* species have reticulate venation (Figure 1G). Studies showed that reticulation in these genera have different origins (Mitsuta 1977). In *Cyrtomium* the reticulations have either a costal or a discal origin, whereas in *Phanerophlebia* they are exclusively marginal (W.H. Wagner 1979). The areolae formed by the reticulations in *Cyrtomium* all have one or two (often three) free excurrent veinlets on which the sori are borne. In *Phanerophlebia* the areolae have no included veinlets.

ANATOMY

Rhizome: stelar structure

The stelar structure of the *Polystichum* rhizome can best be classified as a dictyostele as defined by Schmid (1982). By this definition, two or more perforations (leaf, root or branch gaps) overlap along the vascular cylinder. In those *Polystichum* species with the erect rhizome type, the number of vascular bundles or meristeles (leaf, root and branch traces excluded) may number as many as eight (Figure 2A). In the decumbent rhizome type, however, the number is typically lower at four or five (Figure 2B), but in *P. monticola* up to seven vascular bundles may occur. These bundles are variable in size and shape and are situated approximately in a medial ring.

The rhizome of *Cyrtomium falcatum* is a radially symmetrical dictyostele but here only three traces vascularise each frond; the lowest one diverging into the abaxial region of the frond axis and the other two traces into the adaxial region of the frond axis (Gibson *et al.* 1984).

The rhizome branch trace in *P. transkeiense* is a strand that originates laterally from one of the larger vascular bundles of the main axis. This trace is dorsoventral and haplostelic as defined by Schmid (1982). The first frond borne by this rhizome branch is not associated with a leaf gap. However, when the second and third fronds develop, non-overlapping leaf gaps are formed. At this stage the stele is still dorsoventral. A true dictyostele is established later.

Root traces branch at irregular distances off the dorsal or lateral surfaces of the main axis vascular bundles and are not associated with root gaps. Chandra & Nayar (1982) claim that they originate from the base of the leaf trace as well, but we were unable to confirm this. The stele in the roots of most species is circular in cross section, whereas in *P. lucuosum* it is often conspicuously elliptic with the protoxylem centres forming the distal poles. In all the *Polystichum* species studied the roots were found to be consistently diarch and exarch (Figure 2C, D). In *Cyrtomium caryotideum* var. *micropterum*, a taxon often included in *Polystichum* (Kramer 1990), the roots were found to be triarch.

Frond: stelar structure of the axes

The stelar structure of the stipe base is characterised by four to five (rarely seven) vascular bundles arranged in a U-shape towards the adaxial surface. Khullar & Gupta (1979) reported up to nine vascular bundles in *P. biaristatum* (Blume) T.Moore, whereas smaller species like *P. obliquum* (D.Don) T.Moore merely have two. In *Polystichum* the arc is a broken line with the larger vascular bundles located in a dorsolateral position at either end and the smaller ones between (Figure 2E). The smaller vascular bundles are the first to branch from the lateral ends of two adjacent rhizome meristeles and the larger ones are the last to branch from the rhizome meristeles. A reduction in the number of vascular bundles usually takes place along the length of the stipe as some of the smaller bundles merge. An increase often occurs as a bundle may also split to fuse again after a short distance. The xylem strand in the larger meristeles is curved and hooked adaxially, the so-called hippocampus shape when viewed in cross section (Lin & De Vol 1977) (Figure 2F). Xylem bundles in the smaller meristeles are circular to broadly elliptic in cross section. In *Dryopteris* we observed a consistently larger number of vascular bundles (up to 12) in the stipe.

Xylem tissue in the vascular bundles is composed of helical and scalariform tracheids with thin plates of xylem parenchyma irregularly dispersed between them. Protoxylem of the smaller and larger vascular bundles has an endarch arrangement. The phloem, which forms a sheath around the xylem, is more prominent in the outer dorsolateral and ventral sides of the xylem. The pericycle consists of large parenchymatous cells two to four cell layers deep. The endodermis is characterised by inner and radial walls that are secondarily thickened and in which numerous simple and branched pits of variable sizes are scattered. Pit apertures are always elliptic in outline.

In all the species of the Dryopterideae studied the arrangement of the vascular tissue in the rachis is essentially the same as that of the stipe. In the rachis, however, there is a further reduction in the number of vascular bundles towards the lamina apex. Also here the smaller bundles initially merge with one another at irregular intervals and often also divide as in the stipe. The final small bundle eventually merges with one of the larger dorsolateral bundles some distance from the lamina apex. The two dorsolateral meristeles eventually fuse and continue as a single vascular bundle to the lamina apex (Figure 2J).

The vascular tissue serving each pinna, branches as a single dorsolateral trace from one of the two larger vascular bundles. This trace soon divides and the two (rarely three) bundles that are formed run parallel to one another for most of the pinna length before they finally merge near the pinna apex. This condition holds true for 1-pinnate species and those with more compound laminae suggesting the costa of 1-pinnate species to be analogous with the secondary rachis of species with more compound laminae. Costules and veins branch from one of the two pinna meristeles or the terminal bundle of the pinna apex and remain single-stranded.

Rhizome: non-vascular tissue

In most of the species investigated the non-vascular tissue of the rhizome is distinctly differentiated into parenchymatous ground tissue and sclerenchyma. Histologically the cortex and pith are identical, consisting of small isodiametric parenchyma cells. Towards the epidermis, however, the cells become compressed with the anticlinal walls somewhat sinuate. A narrow sheath of sclerenchyma several cell layers deep is situated beneath the epidermis. In the outer cortical layer this sclerenchyma usually extends to the root trace. In *P. transkeiense* a small sclerotic cap is formed on the outer periphery of the root trace only, whereas in *P. dracomontanum* and *P. incongruum* a sclerotic sheath often forms around the entire root trace. Chandra & Nayar (1982) also found sclerenchyma bundles associated with the departing leaf trace bundles. Small to large groups of partially to moderately thick-walled sclerenchymatous cells occur at random throughout the ground tissue of most species and often extend to the stipe bases. Their abundance appears to be determined by age and the environment with more cell aggregates present in older parts of the rhizome as well as in plants occurring in exposed habitats. In older rhizomes they appear to be concentrated near the larger meristeles. Considering the abundance and distribution of sclereid clusters in the ground tissue of the rhizome, Chandra & Nayar (1982) suggested some evolutionary trends and species relationships within *Polystichum*. D.H. Wagner (1979) also found the presence of sclereid clusters in the rhizome of *P. munitum* (Kaulf.) C.Presl diagnostic in separating it from *P. imbricans* (D.C.Eaton) D.H.Wagner where they are mostly absent. However, because of their variability, we consider them to be of no taxonomic value for the species we studied. The deposition of phenolic substances in the sclerenchymatic clusters in especially the older parts of the rhizome may act as a preservative against decay, thus promoting longevity.

The cortex of *Polystichum* roots is composed of a dense inner sclerenchymatic sheath and parenchymatous outer cortex. In old roots the outer non-sclerotic cortical layer decomposes. Sclerenchyma cells opposite the protoxylem poles are generally not as strongly lignified as the rest of the sheath (Figure 2D). Schneider (1996) terms these non-sclerotic cells opposite the protoxylem poles passage cells, a feature that characterises the *Davallia* type of root.

Frond: non-vascular tissue

In cross section the stipe base is usually circular, tetragonal or transversely broadly ovate in outline. In the upper part of the stipe, however, the adaxial surface is usually variously sulcate, as is the rachis. In cross section the epidermal cells are small and isodiametric in outline and their walls generally densely lignified, similar to the underlying band of sclerenchyma. In young material this layer is interrupted dorsolaterally by the aerophore lines studied by Davies (1991). In younger fronds the lateral aerophore lines are composed of parenchymatous cells with large intercellular spaces and are usually not very rich in phenolic substances. With age, however, this tis-

sue also becomes sclerified. Stomata occurring on the stipe and rachis are confined to the aerophore line and may be raised but are mostly flush with the epidermis. A tanniferous sclerenchyma layer is deposited on the inner tangential and radial walls of the cell layer adjoining the endodermis. The density of this layer is determined by age with that in older fronds being more prominent.

The lamina anatomy of species with 1-pinnate fronds differs slightly from those species with more compound laminae. In cross section the pinnules are flat with a shallow V-shaped sulcus adaxially along the costa that has slightly raised margins. The costa and veins that are situated equidistant between the adaxial and abaxial surfaces are enveloped by a narrow layer of parenchymatous tissue, a bundle sheath, that stretches from the adaxial to the abaxial epidermis. This tissue becomes lignified as the frond ages. In *P. macleae*, a 1-pinnate species, the pinna structure is similar except that the costa is significantly enlarged abaxially. This enlarged costa is composed of parenchymatous mesophyll in which the two vascular strands that run parallel to each other occur.

Epidermal cells

Epidermal cells can provide many characters of taxonomic value (Stace 1984), such as cell size, shape, orientation and anticlinal wall undulation. Cell size, however, may be influenced by ploidy level and environmental factors (Metcalf & Chalk 1950).

Epidermal cell size in *Polystichum* has been studied by Chandra (1977), who concluded that *Polystichum* has a closer affinity with *Cyrtomium* than it has with *Arachniodes* and *Dryopteris*. Epidermal cells in all the species of this investigation are elongated parallel to the veins and are irregular in shape. Cell size of the adaxial

and abaxial epidermis differ, those of the abaxial epidermis usually being larger. The anticlinal walls of the epidermal cells are generally sinuous to deeply lobed (Figure 2H), but in *P. crinulosum* (Desv.) J.P.Roux the cells walls are almost straight (Figure 2G). Epidermal cells occurring abaxially along the veins are generally narrow and their anticlinal walls are not as deeply sinuate as those of the intercostal cells. Cell size varies considerably between species, with the smallest cells in *P. ammifolium* and the largest in *P. wilsonii* (Table 2).

Stomata

Stomatal ontogeny in pteridophytes has been studied by Mickel & Lersten (1967), Pant & Khare (1969), Sen & Hennipman (1981) and Mehra & Soni (1983) to name a few. The most comprehensive studies on the morphology of the mature stomatal complex are those of Van Cotthem (1970), Sen & Hennipman (1981) and Mehra & Soni (1983).

Stomata in *Polystichum* are confined to the abaxial surface of the lamina and are positioned in the same plane as the epidermal cells, oriented with their longitudinal axis parallel to the lateral veins (Figure 2I). Anomocytic, eupolocytic, copolocytic and staurocytic stomata have been reported for *Polystichum* (Van Cotthem 1970; Chandra 1977; Mehra & Soni 1983). In the species dealt with here, we found eupolocytic stomata to be the most common type, followed by the anomocytic state. A few copolocytic stomata were noted in *P. aculeatum* (L.) Roth, *P. dracomontanum*, *P. falcinellum*, *P. incongruum* and *P. kalambaitrense*. Guard cell length is fairly variable: the smallest stomata were recorded in *P. crinulosum* and the largest in *P. falcinellum* (Table 3). In *P. setiferum* stoma initials often abort during early development. Stoma size appears to be related to ploidy level (Table 3).

TABLE 2.—Adaxial epidermal cell length in *Polystichum*

Taxon	Range and mean (µm)	SD	N
<i>aculeatum</i> (L.) Roth	78–(116.33)–230	25.93	60
<i>ammifolium</i> (Poir.) C.Chr.	36–(69.88)–108	16.08	100
<i>crinulosum</i> (Desv.) J.P.Roux	62–(86.90)–108	15.62	10
<i>dracomontanum</i> Schelpe & N.C.Anthony	40–(90.04)–200	31.20	100
<i>drepanum</i> (Sw.) C.Presl	64–(90.77)–166	17.81	90
<i>falcinellum</i> (Sw.) C.Presl	70–(135.17)–210	25.26	70
<i>incongruum</i> J.P.Roux	56–(103.2)–206	27.50	100
<i>kalambaitrense</i> Tardieu	82–(134)–176	29.01	20
<i>kilimanjaricum</i> Pic.Serm.	92–(134)–244	30.86	30
<i>luctuosum</i> (Kunze) T.Moore	68–(110.9)–162	19.36	100
<i>macleae</i> (Baker) Diels	40–(85.48)–136	18.65	100
<i>maevaranense</i> Tardieu	102–(136)–176	20.24	10
<i>magnificum</i> F.Ballard	82–(127.34)–196	26.08	70
<i>marionense</i> Alston & Schelpe	44–(90.63)–166	26.80	60
<i>monticola</i> N.C.Anthony & Schelpe	62–(117.02)–196	28.99	100
<i>pauciaculeatum</i> Bonap.	56–(95.5)–170	23.31	100
<i>pungens</i> (Kaulf.) C.Presl	62–(111.7)–204	29.88	100
<i>setiferum</i> (Forssk.) T.Moore ex Woyn.	50–(88.57)–124	16.52	100
<i>transkeiense</i> W.B.G.Jacobsen	50–(87.3)–138	17.44	100
<i>transvaalense</i> N.C.Anthony	82–(138.85)–226	27.01	100
<i>tsaratananense</i> Tardieu	62–(105.46)–154	23.91	30
<i>volkensii</i> (Hieron.) C.Chr.	64–(113.06)–176	23.63	60
<i>wilsonii</i> H.Christ	76–(147.38)–284	39.82	100
<i>zambesiicum</i> Schelpe	44–(78.16)–196	20.85	100
× <i>maderense</i> J.Y.Johnson	52–(124)–210	41.86	40
× <i>saltum</i> J.P.Roux	128–(173.44)–248	31.56	50

SD, standard deviation; N, number of observations.

TABLE 3.—Guard cell length in *Polystichum*

Taxon	Range and mean (µm)	SD	N	Ploidy
<i>aculeatum</i> (L.) Roth	40–(51.48)–62	4.54	400	tetraploid
<i>ammifolium</i> (Poir.) C.Ch.	32–(40.94)–50	3.44	500	–
<i>crinulosum</i> (Desv.) J.P.Roux	30–(38.36)–44	3.17	50	–
<i>dracomontanum</i> Schelpe & N.C.Anthony	34–(49.54)–65	5.41	500	–
<i>drepanum</i> (Sw.) C.Presl	36–(45.16)–56	3.46	500	tetraploid
<i>falcinellum</i> (Sw.) C.Presl	42–(61.76)–76	5.06	500	octoploid
<i>incongruum</i> J.P.Roux	34–(47.46)–76	6.90	500	tetraploid
<i>kalambatiense</i> Tardieu	50–(56.8)–70	3.41	100	–
<i>kilimanjaricum</i> Pic.Serm.	40–(53.96)–70	5.75	150	–
<i>luctuosum</i> (Kunze) T.Moore	34–(42)–52	3.76	500	triploid
<i>macleae</i> (Baker) Diels	32–(46.03)–60	5.49	500	tetraploid
<i>maevaranense</i> Tardieu	46–(52.76)–60	3.07	50	–
<i>magnificum</i> F.Ballard	50–(56.1)–64	3.13	100	–
<i>marionense</i> Alston & Schelpe	22–(46.82)–64	5.62	300	–
<i>monticola</i> N.C.Anthony & Schelpe	30–(54.08)–70	6.36	1000	hexaploid
<i>pauciaculeatum</i> Bonap.	30–(43)–54	4.54	500	–
<i>pungens</i> (Kaulf.) C.Presl	38–(50.33)–68	5.62	500	octoploid
<i>setiferum</i> (Forsk.) T.Moore ex Woy.	20–(39.37)–52	3.63	300	diploid
<i>transkeiense</i> W.B.G.Jacobsen	32–(42.94)–54	3.86	500	tetraploid
<i>transvaalense</i> N.C.Anthony	22–(48.93)–62	3.96	500	tetraploid
<i>tsaratananense</i> Tardieu	28–(39.38)–46	3.07	100	–
<i>volkensii</i> (Hieron.) C.Ch.	36–(48.79)–56	4.08	200	–
<i>wilsonii</i> H.Christ	38–(56.46)–74	5.83	500	tetraploid
<i>zambesiaceum</i> Schelpe	28–(43.88)–56	3.69	500	–
× <i>maderense</i> J.Y.Johnson	46–(57.92)–66	3.46	100	pentaploid
× <i>saltum</i> J.P.Roux	54–(59.68)–66	3.24	50	tetraploid

SD, standard deviation; N, number of observations.

CONCLUSIONS

This study illustrates our poor understanding of the genus *Polystichum*, like other polystichoid ferns, is characterised by a set of features, most of which are also shared by other members within the assemblage, rather than a set of unique characters (Table 4). The genus can, however, be readily distinguished by an adaxially sulcate rachis with four to five (rarely seven) vascular bundles arranged in a U-shape, axes that are adaxially shallowly sulcate, the sulcus of the secondary axes confluent or not with that of the main axis, 1-pinnate to 3-pinnate fronds with (mostly) adscopically developed pinnae and pinules, anadromous free venation, indumentum composed of paleae (rarely also clavate glandular hairs), sori occurring dorsally on the veins or at a vein apex, and a peltate indusium (secondarily lost in a number of species).

In *Polystichum* the short, erect rhizome type is the most common, occurring in a wide range of taxa of which many are not considered related and is also widespread in the other polystichoid genera. Species belonging to this group are mostly forest dwelling and occur as individuals. Species in the second rhizome type can reproduce vegetatively and have the ability to grow in a wider range of habitats. This clone-forming group can consequently be found growing in forests, forest margins or open habitats. The sharing of resources by clone-forming plants (Hutchings 1997) may compensate for the fewer fronds produced by each rhizome branch.

Chandra & Nayar (1982) and D.H. Wagner (1979) consider the presence and distribution of sclerenchymatic cell aggregates in the cortex and pith of the rhizome of taxonomic value. Our observations, however, suggest their presence and number is influenced by age and habitat and we consequently consider them of no taxonomic value.

Root morphology and anatomy also appear to have little taxonomic value at the species or genus level. In *Polystichum* both the *Dennstaedtia* type and *Davallia* type of cortex occur (Schneider 1996). These root types are widespread within the Pteropsida occurring in several groups generally not considered related. The latter type, characterised by the presence of passage cells opposite the protoxylem poles, we observed in *P. luctuosum* only. All species had diarch roots apart from *Cyrtomium caryotideum* var. *micropterum*, where triarch roots were observed, a feature that requires further study.

Fron morphology in African *Polystichum*, as in most polystichoid ferns, is of the monomorphic type. Only in *Dryopteris*, however, do several species have dimorphic fronds. This derived feature is widespread and within the Pteropsida must have arisen independently on numerous occasions. The morphology and anatomy of the axes in polystichoid ferns also exhibit some important evolutionary trends. Holttum (1959) considered the external shape of the rachis and the way in which the shape is modified when a secondary rachis is attached to it, of significant evolutionary and taxonomic importance. He used this feature in separating fern groups with a similar habit and sori. Our observations in *Polystichum*, however, show that this feature exhibits intra- and interspecific variation in the pinnae stalks often being terete rather than sulcate. The pinna sulcus is thus not confluent with that of the rachis. The large number of small vascular bundles in the stipe and rachis of *Dryopteris* taxa we studied appears to be unique within the Dryopterideae, suggesting it to be of taxonomic value, but the evolutionary significance of this is not understood. The secondary rachis being homologous with the costa in 1-pinnate species of polystichoid ferns suggests frond simplification to be derived (Mitsuta 1977; Yatskievych 1989, 1996).

TABLE 4.—Summary of some morphological and anatomical character trends in the rhizome and frond of polystichoid ferns based on species studied and a literature survey

	<i>Arachniodes</i>	<i>Cyrtomium</i>	<i>Dryopteris</i>	<i>Phanerophlebia</i>	<i>Polystichum</i>
Rhizome	erect/decumbent	erect	erect/decumbent	erect	erect/decumbent
Roots	diarch	diarch/triarch	diarch	diarch	diarch
Lamina	1-pinnate to 3-pinnate	simple/1-pinnate	1-pinnate to 3-pinnate	simple to 1-pinnate	1-pinnate to 3-pinnate
Pinna symmetry	mostly basicopic	mostly acroscopic	mostly basicopic	mostly acroscopic	mostly acroscopic
Stipe vascular bundles	4–6	4–6	up to 12	4–6	2–9
Bulbils	?absent	absent	absent/present	absent/present	absent/present
Venation	free	reticulate	free/reticulate	free/reticulate	free*
Dromy	anadromous	anadromous	anadromous/catadromous	anadromous	anadromous
Frond morphism	monomorphic	monomorphic	monomorphic/dimorphic	monomorphic	monomorphic/dimorphic
Axes sulci	confluent/?not	not confluent	not confluent	not confluent	confluent/not
Stomata	mostly anomocytic	mostly eupolocytic	mostly eupolocytic	mostly eupolocytic	mostly eupolocytic

* Depending on the circumscription of the genus, for example *P. dubium* (Karst.) Diels has reticulations.

Within the polystichoid ferns as defined earlier, only certain *Polystichum* and *Dryopteris* species have the ability of producing bulbils on the laminae. In these genera one or more bulbils are mostly borne on the rachis behind the apical pinna. In the West Indies, however, most of the *Polystichum* species bear bulbils, either at a retuse apex of the terminal pinna or at the apex of an extended rachis. The ability to produce bulbils is here viewed as a derived feature. The distinct way in which the bulbils are borne suggest that this feature has also arisen independently on more than one occasion in *Polystichum*.

Ontogenetic studies show that monopodially branched free veins are ancestral and that reticulate venation within the polystichoid ferns is derived (Mitsuta 1977). It is widely accepted that reticulate veins are derived independently in *Cyrtomium* and *Phanerophlebia*. Yatskievych (1996) is also of the opinion that within *Phanerophlebia* it arose independently on two occasions. Sorus-bearing veins terminating near the lamina margin are here considered ancestral, whereas modified veins terminating in the sorus or extending for a short distance beyond the sorus are considered derived.

The epidermal cell anticlinal walls show considerable variation in the degree to which they are undulated and are here not considered to be of any taxonomic value. Polystichoid ferns are all hypostomatic, and the stomata are mostly of the anomocytic type. Our observations confirm that within closely related species ploidy level is reflected in the guard cell length as *P. pungens*, an octoploid (pers. obs.) has larger stomata than *P. incongruum* which is tetraploid (Table 3).

Judging by the information provided, more detailed studies on a wider range of species are required if a better understanding of *Polystichum*, and its affinity with the other genera in the Dryopterideae is to be formed. Further studies may reject or support some of the speculative evolutionary trends proposed here. The view of Yatskievych (1989) who suggested *Polystichum* to be polyphyletic, is supported here.

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The epidermis in *Passerina* (Thymelaeaceae): structure, function and taxonomic significance

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Keywords: anatomy, cuticle, epicuticular waxes, epidermis, *Passerina*, southern Africa, stomata, taxonomy, Thymelaeaceae

ABSTRACT

Epidermal features were studied in all 17 species of *Passerina*, a genus endemic to southern Africa. Leaves in *Passerina* are inversely ericoid, the adaxial surface concave and the abaxial surface convex. Leaves are inversely dorsiventral and epistomatic. The adaxial epidermis is villous, with unicellular, uniseriate trichomes and relatively small thin-walled cells, promoting flexibility of leaf margins owing to turgor changes. In common with many other Thymelaeaceae, abaxial epidermal cells are large and tanniniferous with mucilaginous cell walls. The cuticle is adaxially thin, but abaxially well developed, probably enabling the leaf to restrict water loss and to tolerate high light intensity and UV-B radiation. Epicuticular waxes, present in all species, comprise both soft and plate waxes. Epidermal structure proves to be taxonomically important at family, genus and species levels. Interspecific differences include arrangement of stomata and presence or absence of abaxial epidermal hair. Other diagnostic characters of the abaxial epidermal cells are arrangement, size and shape, cuticular ornamentation and presence or absence of wax platelets. Two groups of species on the basis of abaxial epidermal cell orientation are recognised. Many leaf epidermal features in *Passerina* are interpreted as structural adaptations to the Mediterranean climate of the Cape.

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INTRODUCTION

The genus *Passerina* L. comprises about 17 species. all endemic to southern Africa (Thoday 1924; Bond & Goldblatt 1984). Despite the now outdated revision by Thoday (1924), taxonomic boundaries in *Passerina* remain a problem, mainly owing to the apparent lack of marked morphological differences between the species. The present paper emanates from a comparative leaf-anatomical survey of the genus, undertaken as part of a monographic study of the group. This survey highlighted the importance of the epidermis as a source of taxonomic evidence.

The combined distribution of all the *Passerina* species is shown in Figure 1. Most species of *Passerina* are

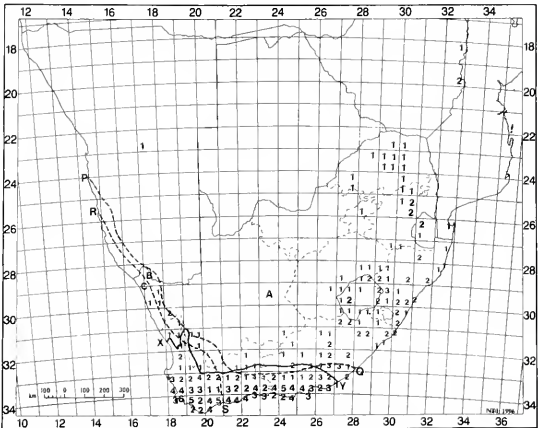


FIGURE 1—Number of species per grid in the distribution of *Passerina*. Lines PQ and RS: boundaries between summer (A), intermediate (B) and winter (C) rainfall areas. Line XY shows northern boundary of Cape Supergroup rock outcrops.

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TABLE 1.—*Passerina* specimens examined and housed at PRE

Species	Collector	Locality
<i>burchellii</i> Thoday	Bredenkamp 1545	WESTERN CAPE.—3319 (Worcester): Jonaskop, (–DC).
	Bolus *687; Stokoe *2542	WESTERN CAPE.—3419 (Caledon): Baviaanskloof, Genadendal, (–BA).
<i>comosa</i> C.H.Wright	Andreue *1288; MacDonald *2125	WESTERN CAPE.—3321 (Ladismith): Seweweekspoort, (–AD).
<i>drakensbergensis</i> Hilliard & B.L.Burt	Edwards 974	KWAZULU-NATAL.—2828 (Bethlehem): Royal Natal National Park, (–DB).
	Bredenkamp *1018, 1019, *1020	KWAZULU-NATAL.—2829 (Harrismith): Ndedema Gorge, Cathedral Peak Forest Reserve, (–CD).
<i>ericoides</i> L.	Bredenkamp *962	WESTERN CAPE.—3418 (Simonstown): Cape Maclear, (–AD).
	Bredenkamp *+956	WESTERN CAPE.—3318 (Cape Town): Milnerton, (–CD).
	Taylor 4042	WESTERN CAPE.—3419 (Caledon): Pearly Beach, (–CB).
<i>falcifolia</i> C.H.Wright	Bredenkamp *+917	WESTERN CAPE.—3323 (Willowmore): Gouna, (–CC).
	Bredenkamp *915	WESTERN CAPE.—3324 (Steytlerville): opposite Tsitsikamma Lodge, (–CD).
	Tyson 1449	WESTERN CAPE.—3423 (Knysna): Knysna, (–AA).
<i>filiformis</i> L.	Killick 238	KWAZULU-NATAL.—2930 (Pietermaritzburg): Table Mountain, (–CB).
	Bredenkamp *1016, *1017	KWAZULU-NATAL.—3030 (Port Shepstone): Oribi Gorge, (–CB).
	Bredenkamp *1012; Van Wyk & Bredenkamp 1	KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Bridge, (–AA).
	Bredenkamp 896	EASTERN CAPE.—3327 (Pедdie): Kiwane, (–BA).
	Bredenkamp 1036	WESTERN CAPE.—3418 (Simonstown): Steenbras River Mouth, (–BB).
<i>galpinii</i> C.H.Wright	Bredenkamp *946	WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD).
	Galpin 4491	WESTERN CAPE.—3421 (Riversdale): Melkhoufontein, (–AD).
	Bredenkamp *932	WESTERN CAPE.—3421 (Riversdale): Riethuiskraal, (–AD).
	Bredenkamp 933	WESTERN CAPE.—3421 (Riversdale): Still Bay, (–AD).
	Bredenkamp 923	WESTERN CAPE.—3422 (Mossel Bay): Mossel Bay, (–AA).
<i>glomerata</i> Thunb.	Bredenkamp *988, 994, 1002	WESTERN CAPE.—3219 (Wuppertal): Cederberg Mountains, near Algeria, (–AC).
	Bredenkamp 984	WESTERN CAPE.—3219 (Wuppertal): Citrusdal, (–CA).
	Bredenkamp 977	WESTERN CAPE.—3219 (Wuppertal): Ceres, Karoo, Farm Groenfontein, (–DC).
	Bredenkamp *973	WESTERN CAPE.—3319 (Worcester): Tulbagh, (–AC).
<i>montana</i> Thoday	Giess 13136	NAMIBIA.—2217 (Windhoek): Awas Mountains, (–CA).
	Bredenkamp 1028	NORTHERN PROVINCE.—2427 (Thabazimbi): Marikela Nature Reserve, (–BC).
	Bredenkamp *1024	MPUMALANGA.—2430 (Pilgrim's Rest): World's View, (–DD).
	Bredenkamp *1025	MPUMALANGA.—2430 (Pilgrim's Rest): God's Window, (–DD).
	Bredenkamp 889, *890	FREE STATE.—2828 (Bethlehem): Golden Gate National Park, (–DA).
	Bredenkamp *893	FREE STATE.—2927 (Maseru): Ladybrand, (–AB).
<i>obtusifolia</i> Thoday	Bredenkamp 971	WESTERN CAPE.—3319 (Worcester): Karoo National Botanical Garden, (–CB).
	Bredenkamp 967	WESTERN CAPE.—3319 (Worcester): Jonaskop, (–CD).
	Bredenkamp 1033, *1034	WESTERN CAPE.—3321 (Ladismith): Seweweekspoort, (–AD).
	Bredenkamp *929	WESTERN CAPE.—3321 (Ladismith): Rooiberg, (–CB).
	Bredenkamp *919	WESTERN CAPE.—3322 (Oudtshoorn): Perdepoort, (–CD).
<i>paleacea</i> Wikstr.	Bredenkamp 960	WESTERN CAPE.—3418 (Simonstown): Kommetjie, (–AB).
	Bredenkamp *+961	WESTERN CAPE.—3418 (Simonstown): Cape Maclear, (–AD).
	Bredenkamp 952	WESTERN CAPE.—3418 (Simonstown): Harold Porter National Botanical Garden, (–BD).
	Bredenkamp 950	WESTERN CAPE.—3420 (Bredasdorp): De Hoop Nature Reserve, (–AD).
	Bredenkamp *949	WESTERN CAPE.—3420 (Bredasdorp): Waenhuiskrans, (–CA).
	Bredenkamp 940	WESTERN CAPE.—3421 (Riversdale): Puntjie, (–AC).
<i>paludosa</i> Thoday	Bredenkamp *1035; Jangle *156	WESTERN CAPE.—3418 (Simonstown): Rondevlei Nature Reserve, (–BA).
	Thoday 100	WESTERN CAPE.—3418 (Simonstown): Riet Valley, Cape Flats, (–BA).
<i>pendula</i> Eckl. & Zeyh.	Fourcade 3040	EASTERN CAPE.—3324 (Steytlerville): Suuranys, (–CB).
	Bredenkamp *908, *909	EASTERN CAPE.—3325 (Port Elizabeth): Groendal Nature Reserve, (–CB).
	Ward 7211	KWAZULU-NATAL.—2832 (Mtubatuba): St. Lucia Park, (–AD).
<i>rigida</i> Wikstr.	Bredenkamp *1013	KWAZULU-NATAL.—3130 (Port Edward): Umtamvuna River Mouth, (–AA).
	Bredenkamp *899	EASTERN CAPE.—3326 (Grahamstown): Kenton-on-Sea, (–DA).
	Bredenkamp 898	EASTERN CAPE.—3326 (Grahamstown): Port Alfred, (–DB).
	Bredenkamp 897	EASTERN CAPE.—3327 (Pедdie): Kleinmond West, (–CA).
	Bredenkamp 911	EASTERN CAPE.—3424 (Humansdorp): Jeffreys Bay, (–BB).
<i>rubra</i> C.H.Wright	Bredenkamp 914	EASTERN CAPE.—3324 (Humansdorp): Kareedouw, (–CD).
	Bredenkamp *905	EASTERN CAPE.—3325 (Port Elizabeth): Colchester, (–DB).
	Bredenkamp *900	EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD).
<i>vulgaris</i> Thoday	Bredenkamp *926	WESTERN CAPE.—3321 (Ladismith): foot of Gysberg Pass, (–CC).
	Bredenkamp 907	EASTERN CAPE.—3325 (Port Elizabeth): Groendal Nature Reserve, (–CB).
	Bredenkamp 901	EASTERN CAPE.—3326 (Grahamstown): Grahamstown, (–AD).
	Bredenkamp 943	WESTERN CAPE.—3420 (Bredasdorp): Bontebok National Park, (–AB).
	Bredenkamp *924	WESTERN CAPE.—3422 (Mosselbaai): Kleinbrak, (–AA).
sp. nov. 1	Bredenkamp *1044, *1046, *1047	WESTERN CAPE.—3319 (Worcester): Waboomberg, (–AD).
sp. nov. 2	Esterhuysen *12189, *26859	WESTERN CAPE.—3218 (Clanwilliam): northern Cederberg Mountains, (–BB).
sp. nov. 3	Stokoe *9302	EASTERN CAPE.—3322 (Oudtshoorn): Swartberg Pass, Prince Albert area, (–AC).
	Esterhuysen *28006	EASTERN CAPE.—3324 (Steytlerville): Cockscornb, (–BD).
sp. nov. 4	Schlechter *9302	EASTERN CAPE.—3322 (Oudtshoorn): Montagu Pass, (–AC).
	Esterhuysen *10734	EASTERN CAPE.—3323 (Willowmore): Kouga Mountains, (–DA).

* Material used for the SEM study of the ad- and abaxial epidermises. +Fresh material collected for the TEM study.

endemic to the Cape Floristic Region. From here the distribution of *P. filiformis* and *P. montana* extends east and north along the eastern mountains and Great Escarpment of southern Africa. In the Cape the climate is for the most part Mediterranean or semi-Mediterranean. In the west, it rains in winter; along the south coast, winter rainfall is complemented by some summer rain which increases eastwards. The western Karoo and Namaqualand (Succulent Karoo Biome) are characterised by winter precipitation and summer drought. KwaZulu-Natal and the eastern mountains of southern Africa are predominantly summer rainfall areas. Distribution of the species of *Passerina* coincides with the geography and climate along the whole distribution area. *P. ericoides*, *P. paleacea*, *P. paludosa*, *P. galpinii* and *P. burchellii* are endemic to Western Cape. The first three species are found along beaches and salt marshes only, *P. galpinii* grows mainly on calcrete in the Agulhas Plain area (Goldblatt & Manning in press) and *P. burchellii* is found on the high mountains at Genadendal and Villiersdorp. *P. comosa* grows on mountain slopes and summits in the Kamiesberg, Great Winterhoek and Klein Swartberg Ranges. *P. glomerata* is found from Worcester to Tulbagh, in the Clanwilliam area and extends to the Witteberg south of Matjiesfontein. *P. obtusifolia* is ubiquitous in the Cape, distributed from Worcester in Western Cape to Alice in Eastern Cape and on some of the mountain ranges in and around the Little Karoo. A new species, of which the plants are often buried under snow during winter, grows at high altitudes in the Ceres Karoo. *P. vulgaris* is a pioneer with a wide distribution from Western Cape to East London in Eastern Cape. *P. falcifolia* is found on mountain ranges between George and Uitenhage and *P. pendula* is endemic to the KwaZungu Catchment Basin and the Zwartkops River area of Eastern Cape. *P. rubra* is common in the Port Elizabeth to Uitenhage area, with outliers in the Swellendam and Bredasdorp Districts. *P. drakensbergensis* is endemic to the high Drakensberg in the Bergville District of KwaZulu-Natal and *P. rigida* is distributed all along the coast, from northern KwaZulu-Natal to the Cape Peninsula. *Passerina* sp. nov. 2 is found on the northern Cederberg Mountains, *P. sp. nov. 3* at mountain tops in the Uitenhage area and the Swartberg Pass and *P. sp. nov. 4* on the Kouga Mountains and the Montagu Pass.

The most important studies applying the 'anatomical method' for the delimitation of the Thymelaeaceae were published by Van Tieghem (1893) and Supprian (1894). The presence of mucilaginous epidermal cells in *P. ericoides* (= *Chymococca empetroides* Meisn.) as opposed to the total lack thereof in the other species, was also mentioned by Supprian (1894). Subsequently, Gilg (1894) critically discussed the 'anatomical method' as applied by Van Tieghem (1893) and Supprian (1894) for the delimitation of the Thymelaeaceae and concluded that certain characters would not uphold criticism. He regarded former systems based on floral morphology as more suitable for a taxonomic grouping of the Thymelaeaceae.

The twentieth century yielded very little anatomical work on the Thymelaeaceae. Standard works were those of Solereder (1908) and Metcalfe & Chalk (1950, 1979). Thoday (1921) described the structure and behaviour in drought of the ericoid leaves of *P. filiformis* and *P. cf.*

falcifolia; he also supplied some notes on their anatomy. In a discussion of inversely dorsiventral leaves, Kugler (1928) included a description of the leaves of *P. filiformis* (= *P. pectinata* Hort.). More recently, leaf anatomy of the genera *Lachnaea* L. and *Cryptadenia* Meisn. was treated by Beyers (1992) and leaf and involucre bract characters of systematic use in *Gnidia* L. were studied by Beaumont *et al.* (1994). The scanty information on leaf anatomy in Thymelaeaceae calls for further research in this field, especially in the genus *Passerina*.

Previous leaf anatomical studies identified mucilagination of the epidermal cells as being of possible taxonomic importance. Recently Bredenkamp & Van Wyk (1999) clarified the structure of the epidermal cells and origin of the mucilage, concluding that mucilagination of epidermal cells is of taxonomic importance mainly at the family level.

The wide distribution of *Passerina* in the Cape Floristic Region, along the southern and eastern coastline and along the Great Escarpment of southern Africa as far north as Zimbabwe, illustrates the adaptation of these plants to a wide range of habitats, including Mediterranean and summer rainfall regimes. Decreasing rainfall from the eastern Escarpment to the northwestern Cape is reflected by adaptive changes in the leaf structure of the group. The present paper provides a description of epidermal characters in *Passerina* as well as an assessment of their taxonomic significance. It also speculates on the possible adaptive value of the observed structural features of the leaf.

MATERIAL AND METHODS

Fresh leaf material of 17 species of *Passerina* (Table 1) was collected, fixed and stored in a 0.1 M phosphate-buffered solution at pH 7.4, containing 2.5% formaldehyde, 0.1% glutaraldehyde and 0.5% caffeine [modified Karnovsky fixative; Karnovsky (1965)]. Whenever possible, material from at least five different localities was collected, fixed and air-dried for each species and herbarium specimens were made.

Light microscope (LM) studies

The LM was used for general leaf anatomy as well as epidermal studies. Unless stated otherwise, the tenth leaf from the growing point of a twig was used in all comparative studies. To prepare transverse sections of the main vein as well as both leaf margins, a 1 mm wide segment of leaf material was cut from the centre of each leaf. Samples were dehydrated, embedded in glycol methacrylate (GMA) and sectioned according to the methods of Feder & O'Brien (1968). Sections were stained with the periodic acid/Schiff's reaction and in toluidine blue 'O', then mounted in Entellan (Art. 7961, E. Merck, Darmstadt).

The following three methods were followed in the study of the cuticles:

1. GMA transverse sections of leaves were stained for 10 minutes in 1% Sudan Black B dissolved in 70% ethanol. Sections were rinsed twice in 70% ethanol for a few seconds and mounted in glycerine jelly.

2. Cuticular mounts were obtained by maceration according to the method of Kiger (1971). Specimens were slightly over-stained in a 1% aqueous safranin solution, dehydrated in methyl cellulosolve and mounted in Entellan.

3. Epidermal mounts were obtained by removing small pieces of ad- and abaxial epidermis manually and by paradermal hand sections. Epidermises were stained in 1% safranin dissolved in 50% ethanol, dehydrated in a graded ethanol series and mounted in Entellan.

Scanning electron microscope (SEM) studies

The SEM was used to study the epidermal surface features (including epicuticular waxes), as well as to verify the structure of the cuticle. Leaves from air-dried material were used for all species. Whole leaves were used as they are small and ericoid, but trichomes were manually removed adaxially to reveal the stomata. Leaves were mounted onto aluminium stubs with silver paint, exposing the ad- and abaxial surfaces separately and sputter-coated with gold. For the purpose of studying epicuticular waxes, the sputter-coating process was modified to prevent high temperatures from changing the wax surfaces. Specimens were sputter-coated for 30 seconds and left to retain their normal temperature for one minute. This was repeated five times after which the specimens were viewed with a Jeol 840 SEM.

For the verification of the authenticity of epicuticular wax droplets and small round protrusions observed in certain species of *Passerina*, leaves were washed in chloroform for one minute, before they were pasted onto aluminium stubs. The procedure described above was used for sputter-coating and viewing.

Transmission electron microscope (TEM) studies

The TEM was used for the study of the structure of mucilaginous epidermal cell walls in *Passerina*. The second, fifth and tenth leaf from the growing points of *P. ericoides*, *P. falcifolia* and *P. paleacea* were used to study the structure of the cell wall. Leaf segments of $\pm 1 \text{ mm}^2$ were fixed in a modified Karnovsky fixative (Karnovsky 1965). Fixed material was rinsed in 0.075 M phosphate buffer, pH 7.4–7.5, post-fixed for one hour in 0.25% aqueous OsO_4 , washed in three changes of water, dehydrated in a graded acetone series and embedded in Quetol 651 resin (Van der Merwe & Coetzee 1992). Ultrathin sections were contrasted in 4% aqueous uranyl acetate for 10 minutes and rapidly rinsed in water three times. The sections were then contrasted with lead citrate (Reynolds 1963), rinsed in water and examined with a Phillips 301 TEM.

For the verification of wettability and possible absorption of water by laminar epidermal hairs, we follow Alvin (1987). He proposed a mechanism through which water is absorbed by the specialised abaxial epidermal trichomes of *Androstachys johnsonii* Prain. This process involves the wettability of the hairs which he investigated by spraying the glabrous adaxial surfaces of the leaves with water. Water seeped round the leaf margins to the abaxial surface, wetting approximately 50%

of the abaxial surface within 5 minutes. In the present study, the glabrous abaxial surfaces of five cymbiform leaves (from dried herbarium specimens) were pasted onto a sticky surface, exposing the villous concave adaxial surface. A drop of water was placed in the adaxial groove at the base of each leaf (average leaf size $2.5 \times 4.0 \text{ mm}$) and left overnight. This experiment was repeated using 0.5% aqueous safranin, followed after 20 minutes by a rinse with water.

Terminology

Trichome structure

We have followed the terminology of Stace (1965) and Theobald *et al.* (1979).

Cuticle

Although the interpretation proposed by Martin & Juniper (1970) for the cuticle of plants has been widely followed by many workers, Holloway (1982) reviewed the historical perspective of the plant cuticle and attempted to adopt the most workable interpretation of the cuticular membrane (CM) in practice. In response, we follow Jeffree (1986), whose uncomplicated and pragmatic interpretation distinguishes three main zones, namely the cuticle proper, the cuticular layer and the cell wall. The cuticular membrane comprises the cuticle proper plus the cuticular layer and is bonded to the outer periclinal walls of the epidermal cells by a pectin-rich layer, which is equivalent to the continuous middle lamella. A layer of epicuticular wax generally coats the cuticle proper.

Cuticular ornamentation (LM and SEM)

We follow Wilkinson (1979) in our choice of terminology to describe cuticular ornamentation.

Epicuticular wax

The recognition of soft waxes in the present study is based on the criteria proposed by Amelunxen *et al.* (1967), Wilkinson (1979) and Barthlott *et al.* (1998).

RESULTS

Macromorphology of the leaf

Leaf arrangement decussate, sometimes imbricate, closely adherent to stem or spreading at angle of 5° – 20° (– 60°); spreading of leaves often prominent in juvenile plants. *Lamina* inversely ericoid; adaxial surface concave, often forming a groove facing stem and lined with woolly hairs; abaxial surface convex, orientated more or less acroscopically, thus exposing a large surface area to the environment; cuticle often amber-coloured (in herbarium material) and outline of epidermal cells often macroscopically visible. *Leaf shape* cymbiform (boat-shaped), falcate or cigar-shaped; plane shape linear, oblong, lanceolate, ovate or trullate. *Leaf base* sessile or cuneate. *Leaf apex* truncate and hump-backed, obtuse, rounded, acuminate

nate or acute to almost spine-tipped. *Margins* sometimes ciliate. *Size* (1.5–)2.5–4.0(–8.0) × (0.8–)1.2–2.0(–3.0) mm.

Anatomy of the leaf

Transverse section (LM): *leaves* epistomatic. *Adaxial epidermis* concave, villous, with unicellular, uniseriate trichomes; cuticle relatively thin, 2–5 µm; epidermal cells uniserial, relatively small (10–)15–25(–35) × 10–17(–20) µm; vacuoles large with tanniniferous substances, cell walls thin; stomata present, with guard cells at same level, sunken below, or raised above adjacent epidermal cells. *Abaxial epidermis* convex, glabrous or sparsely hairy; cuticle relatively thick (10–)20–40(–70) µm; epidermal cells relatively large, periclinal diam. of cells (20–)30–60(–65) µm, anticlinal diam. (25–)30–75 (–105) µm (Table 2), tanniniferous, often with mucilaginous cell walls. *Mesophyll* inversely dorsiventral (Kugler 1928); spongy parenchyma situated adaxially and palisade parenchyma abaxially. *Main vascular bundle* collateral, surrounded by parenchymatous bundle sheath with ample amounts of tanniniferous substances; bundle sheath adaxially irregularly biseriate, abaxially strengthened by sclerenchyma. *Secondary vascular bundles* ± 6; bundle sheaths irregular, parenchymatous and tanniniferous. Figure 2A, B.

Adaxial (dorsal) epidermis

Cuticle

Transverse section (LM): cuticular membrane 2–5 µm thick, smooth, ridged along boundaries of guard cells (Figure 2G), gradually thickening close to leaf margins, equalling abaxial cuticle in thickness and sculpturing at margins.

Surface view (LM and SEM): smooth (Figure 2C), except in *Passerina* sp. nov. 1, where markings on epicuticular wax are most probably caused by snow (Figure 3D, E).

Epidermal cells

Transverse section (LM): cells uniserial, irregularly shaped, relatively small with periclinal diam. (10–)15–25(–35) µm, anticlinal diam. 10–17(–20) µm; cell walls thin, outer periclinal wall convex; vacuoles large, containing tanniniferous substances (Figure 2A, F–H). Margin formed by a few rows of conically shaped or anticlinally elongated cells.

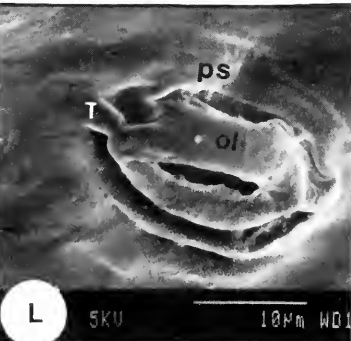
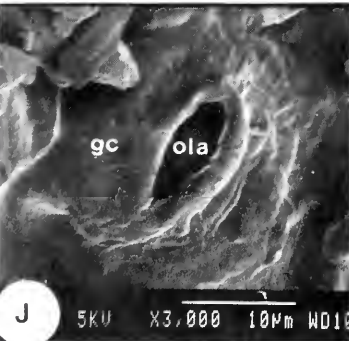
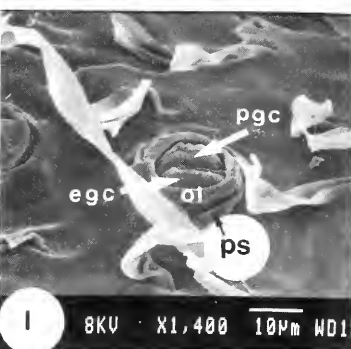
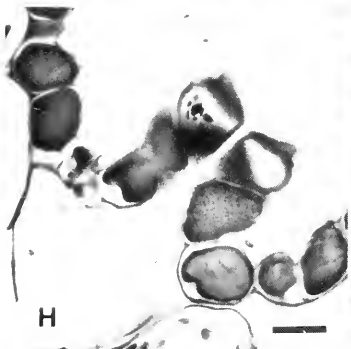
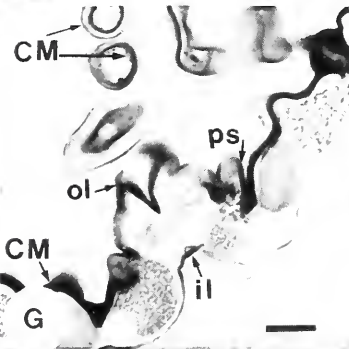
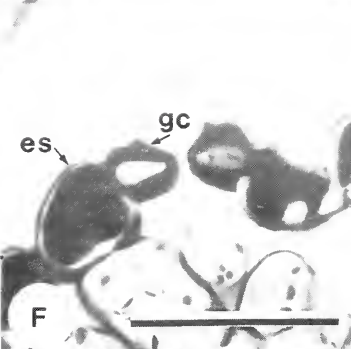
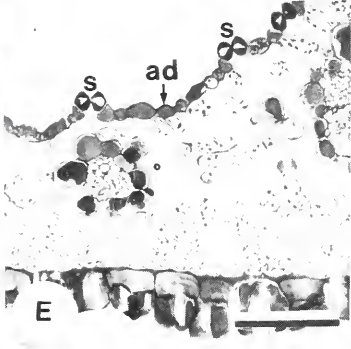
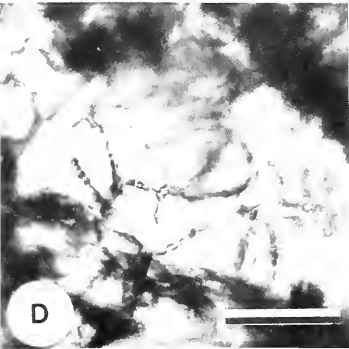
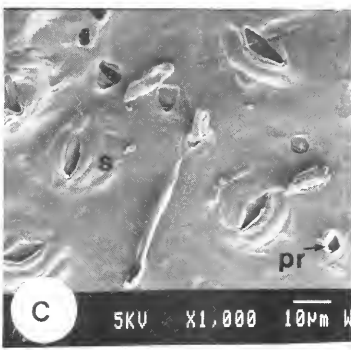
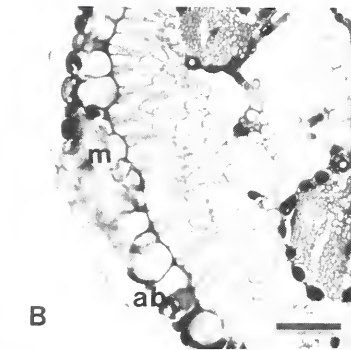
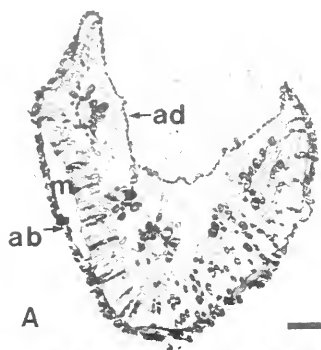
Surface view (LM and SEM): cells polygonal, 4–many-sided, walls usually undulate with loose, wide u-shaped curves of shallow amplitude (Figures 2D, K; 3C), arranged in rows and straight-walled in *Passerina* sp. nov. 1 (Figure 3D, E). Nodular walls observed in *P. falcifolia* (Figure 2D). Vacuoles with ample tanniniferous substances.

Stomatal complex

Transverse section (LM): *lamina* epistomatic; stomata dispersed randomly over adaxial surface, but absent from edges of leaf margin; raised or at same level as other epidermal cells (Figure 2E–H); dispersed in two columns in adaxial epidermal folds, with ± 3–5 rows of epidermal cells in between; raised, sunken or arranged in stomatal crypts in *Passerina* sp. nov. 1 (Figure 3F). *Guard cell* outline in all species varying between widely obtrullate, very widely obtrullate or widely depressed obtrullate, with angles slightly rounded; cell walls thick-

TABLE 2.—Dimensions of abaxial epidermal cells and cuticular membrane (CM) in *Passerina*. Measurements in µm in cross section and surface view

Name	Width of CM	Periclinal diam.	Anticlinal diam.	Length × width	Shape of cell
<i>comosa</i> (Figure 4B, C)	10–40	30–60	70–75	45–55 × 35–40	slightly oblong
<i>glomerata</i>	(20–)30–40(–50)	(20–)30–35(–40)	(25–)30–55(–60)	30–40 × 30–35	isodiametric
<i>ericoides</i> (Figure 4D–F)	20–32	35–60	40–60	35–50 × 40–50	± isodiametric
<i>obtusifolia</i> (Figure 4G–I)	20–30	40–55	55–75(–105)	(30–)40–55(–60) × (45–)50–70(–95)	transversely oblong
<i>burchellii</i> (Figure 4J–L)	60(–70)	45	75	(65–)85(–125) × 45–50	angles rounded, oblong
<i>drakensbergensis</i> (Figure 5A–C)	20	30–35	50–55	50–65 × 30–40	oblong
<i>montana</i> sp. nov. 1 (Figure 5D–F)	30–35 20	30–45 35	45–65 40	40–60 × 35–40 45–55 × 35–40	isodiametric to slightly oblong oblong
<i>vulgaris</i>	(10–)20–30	30–45	35–45(–70)	35 × 30–40	transversely oblong
<i>filiformis</i>	20–35	35(–65)	55–75(–90)	35–55 × 25–30	oblong
<i>falcifolia</i>	20	40	40	60–75 × 35–50	oblong
<i>pendula</i>	30	45–55	60–65	50–65 × 30–40	oblong
<i>rigida</i> (Figure 5G–I)	20–30	35–50	35–55	35–45 × 35–40	isodiametric to slightly oblong
<i>galpinii</i>	40–50	30–35	(40–)55–60(–70)	30–40 × 30	isodiametric to slightly oblong
<i>rubra</i>	20–30	30–50	45	(30–)35(–55) × 35–40	isodiametric to slightly oblong
<i>paleacea</i>	20(–40)	35(–65)	50–60	45–50 × 30–35	slightly oblong
<i>paludosa</i> (Figure 5J–L)	20	35–45	60–70	95–100 × 45–50(–95)	oblong



ened (Figure 2F, H); periclinal and anticlinal dimensions for individual guard cells $10.0\text{--}12.5\text{--}(15.0) \times (10.0\text{--}12.5\text{--}15.0\text{--}(20.0)) \mu\text{m}$. *Cuticular membrane* (Figures 2G; 3B) covering outer periclinal walls of epidermal and guard cells, as well as poral epidermal walls of guard cells, smooth or slightly crenate when lining the pore (Figure 3B), contracted into a pair of \pm continuous outer stomatal ledges above guard cells, thus forming an entire outer cavity (not divided into compartments); inner stomatal ledges and inner cavity present. *Epidermal cells* surrounding guard cells not different from other epidermal cells in size, shape or staining properties (Figure 2F). *Peristomatal cuticular rims* conspicuous on epidermal cells bordering guard cells (Figure 2G).

Surface view (LM and SEM): *stomata* anomocytic; outline elliptic to circular, dimensions $(20\text{--}26\text{--}30\text{--}(35)) \times (15\text{--}24\text{--}30\text{--}(35)) \mu\text{m}$, circular in *Passerina* sp. nov. 1, dimensions $27.5 \times 27.5 \mu\text{m}$. *Epidermal cells surrounding guard cells* 3–5(6), irregularly shaped with sinuate walls and long axis parallel to guard cells, corresponding in orientation, size, shape and staining properties to other \pm elongated epidermal cells (Figures 2D, K; 3C); pentagonal to heptagonal epidermal cells in *Passerina* sp. nov. 1, with walls slightly sinuate to straight, possibly nodular (Figure 3E). *Stomata* raised above or at same level as other epidermal cells in all species (Figure 2I, J, L); dispersed in two columns in adaxial epidermal folds, with \pm 3–5 rows of epidermal cells in between, sunken or arranged in stomatal crypts in *Passerina* sp. nov. 1 (Figure 3D). *Guard cells* often conspicuously raised (Figure 2I, J). *Peristomatal cuticular rims* conspicuous on epidermal cells bordering guard cells (Figures 2I, L; 3A), rims also visible as 1–4 small semilunar protrusions bordering guard cells in cuticular preparations and epidermal peels (Figure 3C) (rims should not be confused with small subsidiary cells, an interpretation which could result in stomata being erroneously classified as paracytic or cyclocytic). *Outer stomatal ledges* \pm continuous, present above guard cells (Figures 2I–L; 3A, C). *Stomatal poles* (where guard cells meet) retuse; T-pieces (cuticular thickenings of common walls between guard cells) well developed (Figures 2I, J, L; 3C).

Trichomes

LM and SEM: *adaxial surface* of leaf villous. *Trichomes* nonglandular, unbranched, devoid of surface features or constrictions, mostly strongly spiralled (Figure 3G, H), terete, with central lumen, covered by cuticle (Figures 2G; 3I). *Hair bases* with pore, poral rim somewhat thickened (Figures 2C; 3C, G); hair base cells most-

ly 4–6 and slightly radially elongated (Figure 3C, G). *Trichomes bordering leaf margin* conspicuous in *P. burchellii*, *P. paludosa* and *P. pendula* (Figure 3I, J). *Trichome foot* scarcely modified, inserted between epidermal cells (Figure 3I), usually straight, but with individual trichomes strongly spiralled (Figure 3J) in *P. pendula* (brown in dried material).

Wettability and the possible absorption of water by the laminar epidermal hairs in *Passerina* were assessed by means of laboratory tests. We found that water had formed a film over the felty layer of hair at the leaf base, whereas the adaxial surface had remained dry. A treatment with 0.5% aqueous safranin revealed that only the exposed parts of the spiralled hairs in the felty indumentum at the leaf bases stained pinkish. Although the longer hairs at the leaf margins were stained, those on the rest of the adaxial surface remained unstained.

Abaxial (ventral) epidermis

Trichomes

Abaxial surfaces of bracts and young leaves in *P. comosa*, *P. sp. nov. 3* and *P. sp. nov. 4* tomentose to sparsely hairy (Figure 4B), older leaves often glabrous. Description of trichomes as described under adaxial epidermis.

Epidermal cells

Transverse section (LM and TEM) (Figures 2A, B, E; 3K–L): epidermis uniserial. *Stomata* absent. *Epidermal cells* more or less oblong in outline; outer periclinal walls straight or convex, inner periclinal walls straight, convex or bulging towards mesophyll, often mucilaginous and then superficially resembling a multiple epidermis; periclinal diam. of cells $(20\text{--}30\text{--}60\text{--}(65)) \mu\text{m}$, anticlinal diam. $(25\text{--}30\text{--}75\text{--}(105)) \mu\text{m}$ (Table 2). *Mucilaginous cell walls* increasing progressively from leaf margin to midrib (Figure 2B), affecting mainly inner periclinal but also anticlinal cell walls (Figure 3K, L); mucilage with a layered appearance (Figures 2E; 3K), eventually occupying about two-thirds of epidermal cell and separated from cytoplasm by innermost cellulose layer of inner periclinal cell wall (Figure 3L). *Cytoplasm* compressed by mucilage, remaining as a thin layer appressed to large, usually tanniniferous vacuole. *Anticlinal layer* of inner periclinal cell wall often plicate but gradually straightening and often disappearing as mucilagination increases, eventually breaking under pressure of accumulating

FIGURE 2.—LM photographs and SEM micrographs of epidermis of inversely ericoid leaf in *Passerina*. A, *P. fulcifolia*, Bredenkamp 917, ad- and abaxial epidermis with mucilage accumulating abaxially; B, *P. galpinii*, Bredenkamp 946, mucilaginous abaxial epidermal cells; C, *P. filiformis*, Bredenkamp 1016, smooth adaxial cuticle, stomata and poral rims of hair bases; D, *P. fulcifolia*, Bredenkamp 915, adaxial epidermal walls undulate, nodular; E, *P. ericoides*, Taylor 4042, stomata at different levels in relation to adaxial epidermis; F, *P. comosa*, Bredenkamp 1034, PAS staining of guard cell walls and surrounding epidermal cells, showing width; G, *P. pendula*, Bredenkamp 909, *vs* adaxial epidermis stained with Sudan Black B, showing cuticular membrane; H, *P. pendula*, Bredenkamp 909, raised stomata stained with toluidine blue; I, *P. paleacea*, Bredenkamp 961, with peristomatal rim, raised epidermal and poral walls of guard cells, conspicuous outer stomatal ledges; J, *P. galpinii*, Bredenkamp 946, with distinct outer stomatal ledge aperture; K, *P. filiformis*, Bredenkamp 1016, and L, *P. pendula*, Bredenkamp 909, with T-pieces at stomatal poles. Abbreviations: ad, adaxial epidermis; ab, abaxial epidermis; CM, cuticular membrane; e, epidermal cell; egc, epidermal wall of guard cell; es, epidermal cell surrounding guard cell; gc, guard cell; ic, inner cavity; il, inner stomatal ledge; l, lumen of trichome; m, mucilage; oc, outer stomatal cavity; ol, outer stomatal ledge; ola, outer stomatal ledge aperture; p, pore; pgc, poral wall of guard cell; pr, trichome poral rim; ps, peristomatal rim; s, stomata; sc, stomatal crypt; t, trichome; T, T-piece at stomatal pole. Scale bars: A, B, D, E, F, K, 100 μm ; C, G, H, I, J, L, 10 μm .

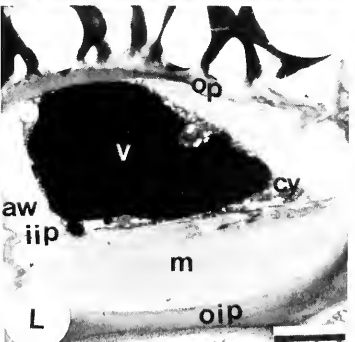
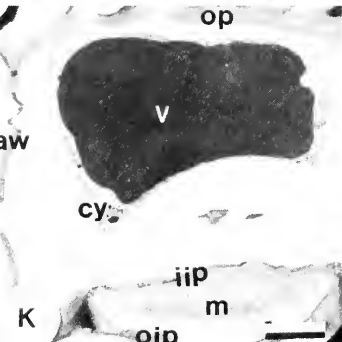
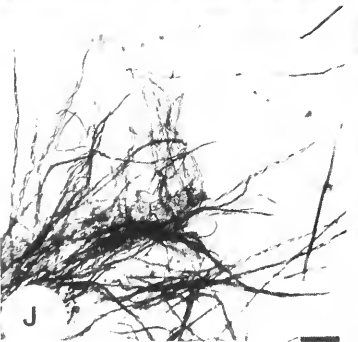
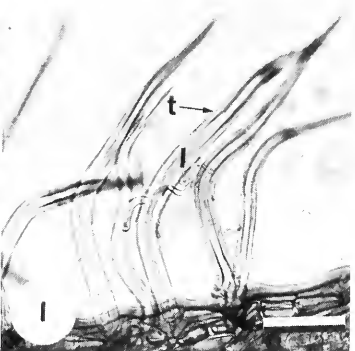
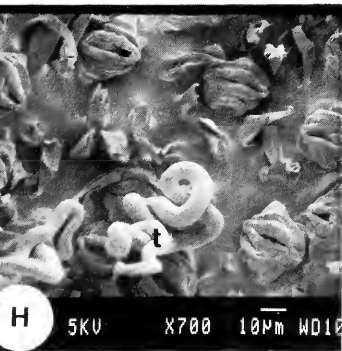
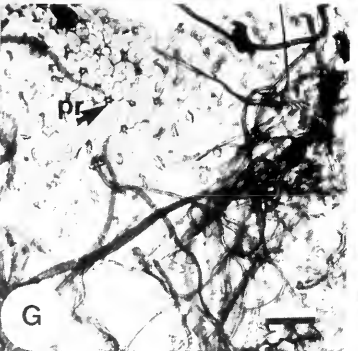
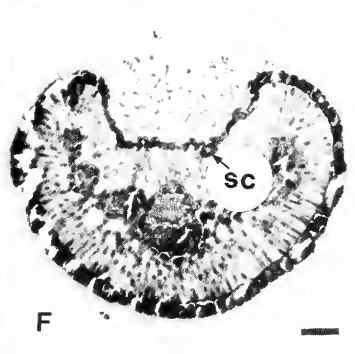
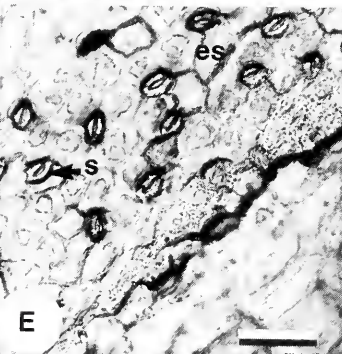
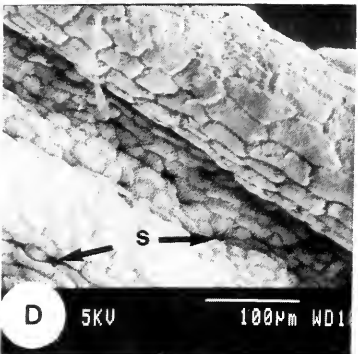
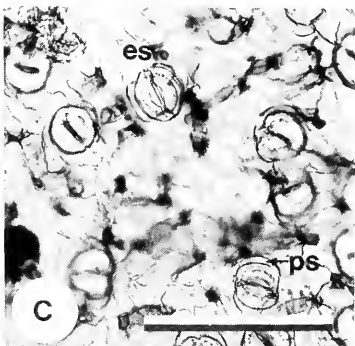
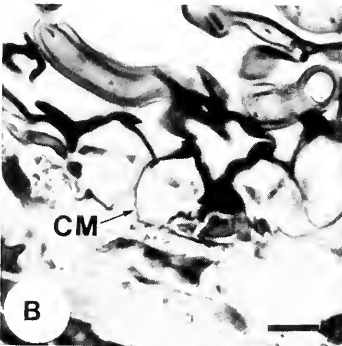


TABLE 3.—Abaxial epidermal characters in *Passerina*

Name	Epidermal cells		Abax- ial hair pre- sent	Ornamentation of CM						Epicuticular		
	random	in rows		Smooth	Papillate				Striate	wax		
					Molar-like crown	One dome per cell	Several domes per cell	Several globular papillae per cell		Soft wax	Platelets	Plates
Group A												
<i>P. glomerata</i> (Figure 6C)	X			X								X
<i>P. ericoides</i> (Figures 4D–F; 6D)	X			X						X		
<i>P. obtusifolia</i> (Figures 4G–I; 6E)	X					X				X		
<i>P. burchellii</i> (Figures 4J–L; 6F)	X						X			X		X
Intermediate												
<i>P. comosa</i> (Figures 4B, C; 6A,B)		X	X		X						X	X
<i>P. sp. nov. 3</i>		X	X				X					X
<i>P. sp. nov. 4</i>		X	X	X				X			X	
<i>P. drakensbergensis</i> (Figures 5A–C; 6G)		X						X				X
<i>P. montana</i>		X		X				X				X
Group B												
<i>P. sp. nov. 1</i> (Figure 5D–F)		X					X					X
<i>P. sp. nov. 2</i>		X					X				X	
<i>P. vulgaris</i>		X							X			X
<i>P. filiformis</i> (Figure 6H)		X							X			X
<i>P. falcifolia</i>		X							X			X
<i>P. pendula</i> (Figure 6I)		X							X		X	X
<i>P. rigida</i> (Figures 5G–I; 6J)		X							X		X	X
<i>P. galpinii</i>		X							X	X		
<i>P. rubra</i>		X							X	X		
<i>P. paleacea</i> (Figure 6K, L)		X							X	X		
<i>P. paludosa</i> (Figure 5J–L)		X							X	X		

mucilage, resulting in a mucilage-filled cavity between remains of epidermal cells and adjacent mesophyll (Figure 2A) (Bredenkamp & Van Wyk 1999).

Surface view (SEM micrographs and cuticular preparations): *shape* pentagonal to heptagonal, cells mostly isodiametric or transversely oblong in *P. glomerata*, *P. ericoides* (Figure 4D, E) and *P. obtusifolia* (Figure 4G, H), but oblong in *P. burchellii* (Figure 4J, K); cells mostly slightly oblong or oblong in all other species of *Passerina* (Figure 5; Table 2). *Arrangement* random in *P. glomerata*, *P. ericoides*, *P. obtusifolia* and *P. burchellii* (Figure 4D–K), in rows in all other species of *Passerina* (Figure 5; Table 3).

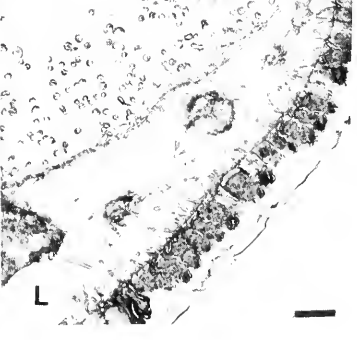
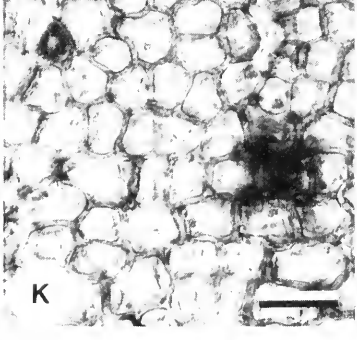
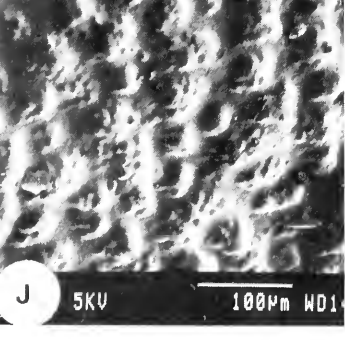
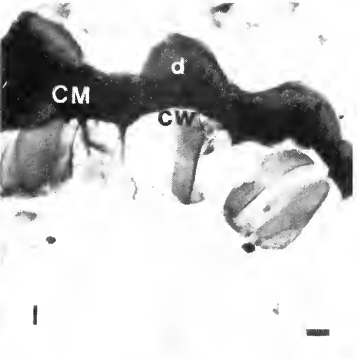
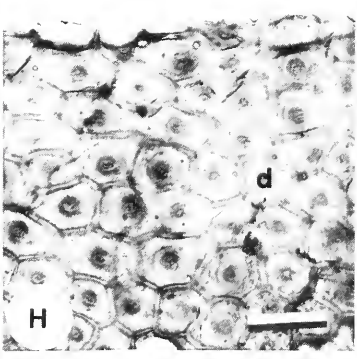
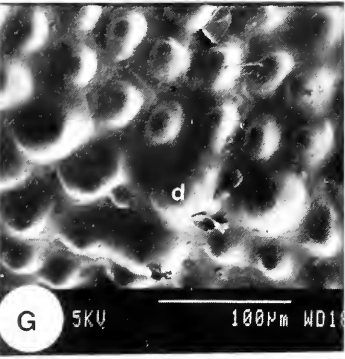
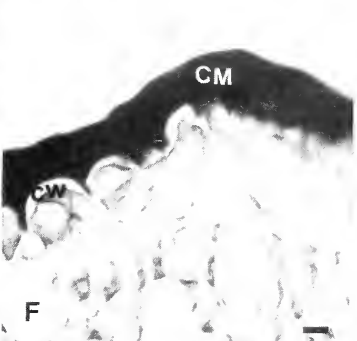
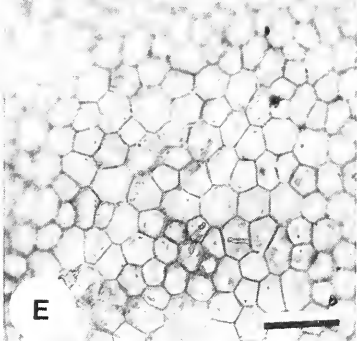
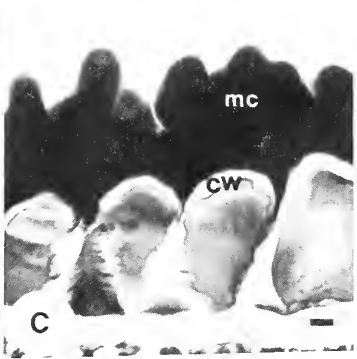
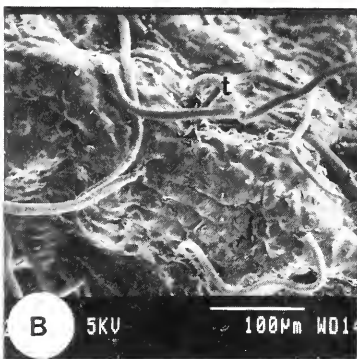
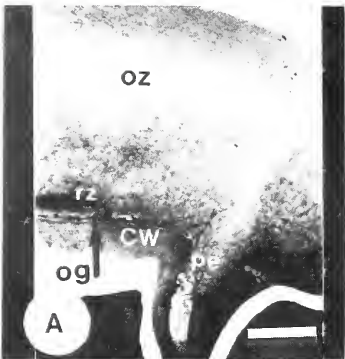
Cuticle

Transverse section (LM): *epicuticular wax* absent owing to chemical treatment during fixation, embedding

and staining. *Cuticular membrane* (CM) well developed, (10–)20–30(–70) µm thick (Table 2); cuticle proper delineated by narrow, lightly stained outer zone and cuticular layer by wider, darker stained zone; cuticular pegs present, formed by layer projecting into grooves between anticlinal walls of adjacent epidermal cells. *Outer periclinal cell walls* not staining with Sudan Black B (Figures 4I; 5C, I, L).

TEM: cuticle structure corresponding to the cuticular structural type 3, described by Holloway (1982). Cuticle proper and CM not distinguishable. *Cuticular membrane* (Figure 4A) comprising a wide, mainly amorphous outer zone and narrow faintly reticulate inner zone; osmophilic granules aligned on border of clearly defined cell wall; cuticular pegs with unknown (possibly pectinaeous) substance (stained light grey) between cell wall and peg, forming part of middle lamella.

FIGURE 3.—LM photographs and SEM micrographs in *Passerina*. A–F, structure of stomatal complex. A–C, *P. rigida*, Bredenkamp 1013, Ward 7211: A, surface view of stomata showing peristomatal rims, raised guard cells and pronounced outer stomatal ledges; B, *t/s* adaxial epidermis stained with Sudan Black B, with crenate surface of cuticular membrane lining poral walls of guard cells; C, epidermal maceration stained with safranin, showing structure of epidermal cells surrounding guard cells, peristomatal rims. D–F, *Passerina* sp. nov. 1, Bredenkamp 1046: D, sunken stomata in cavity of cymbiform leaf; E, epidermal maceration stained with safranin, with structure of epidermal cells and sunken stomata; F, *t/s* leaf, with raised stomata as well as stomatal crypts. G–J, structure of trichomes. G, *P. rubra*, Bredenkamp 905, with poral rims in relation to adaxial epidermal cells. H, *P. falcifolia*, Bredenkamp 915, with unicellular, long, spiralised, pointed trichomes; I, *P. paludosa*, Bredenkamp 1035, with trichome foot and conspicuous lumen; J, *P. pendula*, Bredenkamp 909, trichomes strongly spiralised. K, L, TEM micrographs of abaxial leaf epidermal cells of *P. falcifolia*, Bredenkamp 917, in cross section: K, mucilage accumulated between innermost and outermost cellulose layers of inner periclinal cell wall; L, innermost cellulose layer of inner periclinal cell wall. Abbreviations: aw, anticlinal cell wall; cy, cytoplasm; iip, innermost layer of inner periclinal cell wall; oip, outer layer of inner periclinal cell wall; m, mucilage; op, outer periclinal cell wall; v, vacuole. Scale bars: K, L 5 µm; A, B, H, 10 µm; C–F, G, I, J, 100 µm.



Cuticular ornamentation

In transections and surface view of leaves, LM and SEM studies showed that two groups of species, henceforth called Groups A, Intermediate and B (Table 3), can be distinguished on the basis of the arrangement and shape of epidermal cells as well as cuticular ornamentation.

Group A

Epidermal cells mostly isodiametric or transversely oblong in surface view; arranged randomly; cuticle mostly papillate; *outer periclinal walls* of cells convex in all species. *Cuticular membrane* (CM) smooth in *P. ericoides* and *P. glomerata* (Figures 4D–F; 6C); papillate in *P. obtusifolia*, with one dome per cell, situated \pm centrally on outer periclinal wall of pentagonal or heptagonal cells (Figures 4G–I; 6E); with several domes per cell in *P. burchellii* (Figures 4J–L; 6F).

Group B

Epidermal cells mostly oblong in surface view, arranged in rows; concavities (depressions in centre region of cell) and convexities (rounded cells forming a low dome) more or less alternating (Figure 5G, J); cuticle with ridges at junction of epidermal cell walls mostly conspicuously raised, exhibiting a definite striate pattern (Figure 5D, G, J), otherwise \pm plane.

Cuticular membrane pronounced at junctions of epidermal cell walls and grooved between anticlinal walls of adjacent cells (Figure 5I), more or less smooth in *P. vulgaris*, *P. filiformis*, *P. falcifolia*, *P. pendula*, *P. rigida*, and *P. galpinii*, except in *Passerina* sp. nov. 1, in which the presence of snow, at the time of collecting, seemed to have caused markings on the cuticular wax (Figure 5D, E). Small globular papillae visible between cuticular ridges in *Passerina* sp. nov. 1 (Figure 5D–E), *P. rubra*, *P. paleacea* and *P. paludosa* (Figure 5J–L).

Intermediate

Epidermal cells arranged in rows but CM less pronounced at junctions of epidermal cell walls and cuticular ridges less conspicuous, were recorded in *P. comosa* (Figures 4B; 6A, B), *P. drakensbergensis* (Figure 5A, B), *P. montana*, *P. sp. nov. 3* and *P. sp. nov. 4*. CM smooth or with small globular papillae in *P. montana* and *P. sp. nov. 4*; domed with a 'molar'-like crown in *P. comosa* (Figure 4B, C), with several domes per cell in *P. sp. nov.*

3 and with 9 or 10 globular papillae per cell in *P. drakensbergensis* (Figures 5A–C; 6G).

Epicuticular waxes

Soft waxes present, coating entire abaxial surface: wax protruding through amorphous layer of CM in a variety of configurations: droplets conspicuous in *P. comosa*, *P. ericoides* and *P. burchellii* (Figure 6A, D, F); droplets and small round protrusions forming flat, shapeless lumps in *P. paleacea* (Figure 6L). *Crystalloids*: wax platelets and plates present or absent (Table 3); thin wax platelets, with margins entire or non-entire, flaking from wax surface in *P. comosa* and *P. rigida* (Figure 6A, J) and changing to plates as margins become distinctly edged. Upright plates separating from surrounding wax in *P. filiformis* (Figure 6H). Platelets and plates varying from sparse to abundant; platelets \pm square to irregularly shaped, plates \pm square to oblong and usually arranged perpendicular to cell rows.

The authenticity of epicuticular wax droplets and small round protrusions, observed in *P. ericoides*, *P. obtusifolia* and *P. paleacea* (Figure 7), was verified by washing leaves in chloroform for one minute and comparing them to unwashed specimens under SEM. Epicuticular wax droplets were clearly discernible in unwashed *P. paleacea* (Figure 7A), while small pores appeared in the cleaned, de-waxed cuticle after washing (Figure 7B–E). Similar pores were also present in *P. ericoides* (Figure 7F). No pores were present in the papillate CM of *P. obtusifolia*, but the corroded apices of the papillae clearly showed an accumulation of epicuticular waxes at these points (Figure 7G–I).

DISCUSSION

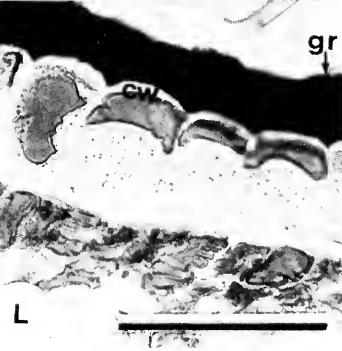
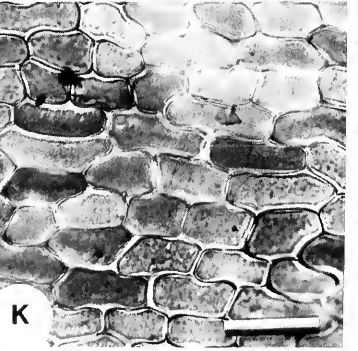
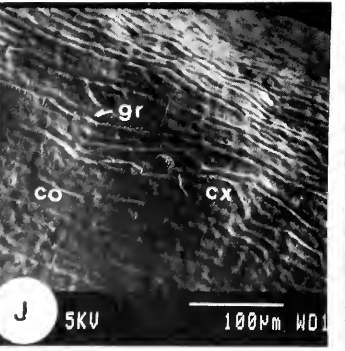
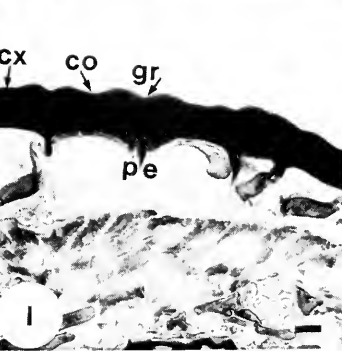
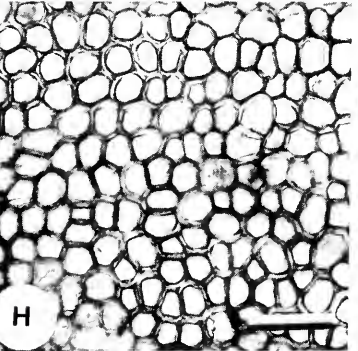
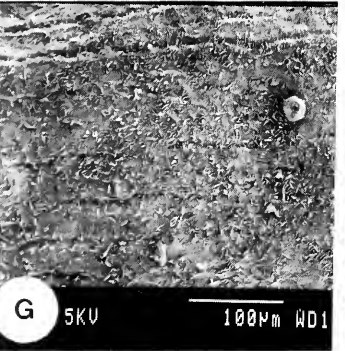
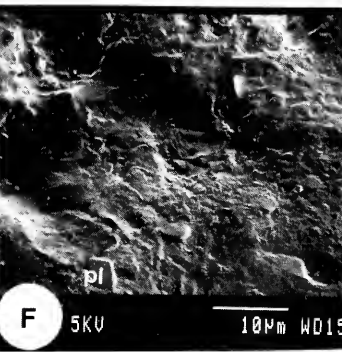
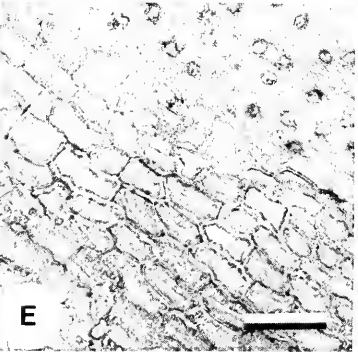
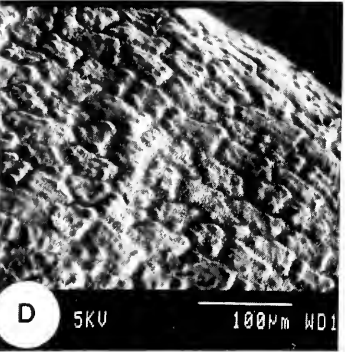
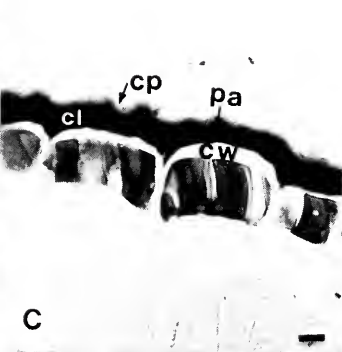
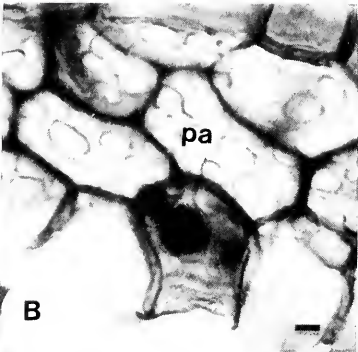
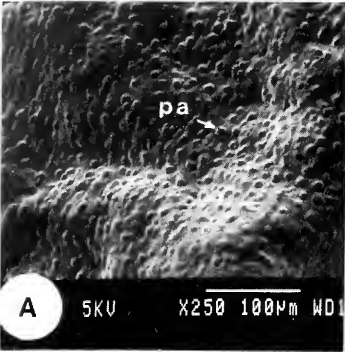
Adaxial epidermis

Plants of high mountains in the tropics usually have straight to curved anticlinal epidermal cell walls, the percentage of species with undulated walls increasing as altitude decreases (Wilkinson 1979). The straight-walled arrangement of the cells in *Passerina* sp. nov. 1 (Figure 3D, E), a high-altitude montane species, seems to comply with this pattern.

Stomatal complex

In all but one species of *Passerina* the stomata are usually raised or at the same level as other epidermal cells (Figure 2E, G, H), indicating that this character is of lim-

FIGURE 4.—A, TEM micrograph of cuticular membrane in *Passerina paleacea*, Bredenkamp 961, with wide, amorphous outside zone, narrow faintly reticulate inner zone, osmiophilic granules at border of cell wall and cuticular peg. B–L, LM photographs and SEM micrographs of abaxial leaf epidermis in *Passerina*. Epidermal macerations stained with safranin and *t/s* of epidermis stained with Sudan Black B. B, C, *P. comosa*, MacDonald 2125, Andraea 1288; B, trichomes present; C, CM domed, with 'molar-like' crown to each dome. D–F, *P. ericoides*, Bredenkamp 956, 962, Taylor 4042; D, CM smooth, epidermal cells randomly arranged, \pm isodiametric, outer periclinal cell walls convex; E, cells randomly arranged, \pm isodiametric; F, convex outer periclinal walls and smooth CM. G–I, *P. obtusifolia*, Bredenkamp 1034; G, CM with one dome per cell; H, epidermal cells randomly arranged, transversely oblong with one dome per cell; I, convex outer periclinal cell wall and CM with one dome per cell. J–L, *P. burchellii*, Bolus 687, Bredenkamp 1545; J, CM with several domes per cell; K, randomly arranged cells, transversely oblong with rounded angles, several domes per cell; L, *t/s* epidermis in polarised light showing CM with several domes per cell. Abbreviations: CM, cuticular membrane; cw, outer periclinal cell wall; d, dome; mc, molar-like crown; og, osmiophilic granules; oz, amorphous outside zone; pe, cuticular peg; rz, narrow faintly reticulate inner zone; t, trichome. Scale bars: A, 5 μ m; C, F, I, 10 μ m; B, D, E, G, H, J–L, 100 μ m.



ited taxonomic value at species level, except in *Passerina* sp. nov. 1, which has stomatal crypts or sunken stomata. Classification of the stomatal complex into stomatal types is often a problem owing to the subtle distinction of subsidiary cells (Wilkinson 1979; Van Wyk *et al.* 1982).

Patel (1978) considers subsidiary cells as morphologically and physiologically different from other epidermal cells and proposes a number of criteria to distinguish subsidiary cells in mature epidermis. Of these criteria we used the following in the distinction of subsidiary cells: size, shape, contents and position of cells. We found that the cells adjacent to the guard cells did not differ from other epidermal cells, except that they might be raised or sunken (Figures 2K; 3C). Furthermore, when stained with PAS, periclinal walls of subsidiary cells should be lightly stained compared with other epidermal cells, owing to less carbohydrates in these cell walls according to Patel (1978). In *Passerina* the periclinal walls of the cells adjacent to the guard cells stained homogeneously with other cells in the stomatal complex (Figure 2F) and the anticlinal walls are not comparatively thinner than those of other epidermal cells, thus the cells adjacent to the guard cells cannot be considered subsidiary cells (Figure 2F, H). Stained with Sudan Black B, the contents of the cells surrounding the guard cells do not differ from those of other epidermal cells and no lipid bodies are present (Figure 2G).

We therefore conclude that the epidermal cells surrounding the guard cells in *Passerina* are not differentiated as subsidiary cells and we classify the stomatal apparatus in *Passerina* as anomocytic. This corresponds to the prevailing state in the Thymelaeaceae (Solereder 1908; Metcalfe & Chalk 1979). However, although we prefer to regard the epidermal cells surrounding the guard cells as similar to other epidermal cells, the presence of conspicuous peristomatal cuticular rims on the outer periclinal cell walls of epidermal cells around the guard cells may be used in support of a view that these cells are subsidiary cells. The stomatal apparatus could then be classified as staurocytic (Wilkinson 1979) or anomotetracytic (Dilcher 1974). As the number of epidermal cells surrounding the guard cells varies from 3–5(6), it would seem appropriate to classify the stomatal apparatus as anomostauroidic (Van Wyk *et al.* 1982).

Trichomes

Passerina leaves are often cymbiform with spiralled trichomes densely arranged in the concave ventral space. This indumentum is likely to play an important

role in the water relations of the plant. Water droplets precipitating from the atmosphere, or running down from leaves directly above, would accumulate in the concave leaf space. Droplets would be repelled by the hydrophobic cuticle of the trichomes and owing to cohesion forces cause a moisture layer in the upper part of the dense trichomes. One may speculate that water vapour escaping through the stomata would not be drawn outwards by capillary forces because of the water-repelling nature of the cuticle surrounding the trichomes, thus retaining a high concentration of moisture in the vicinity of the stomata. The overall high concentration of water vapour over the adaxial surface of the leaf is likely to decrease the transpiration rate. Laboratory tests to assess the wettability and the possible absorption of water by the laminar epidermal hairs in *Passerina*, suggest that the wettability of the spiralled hairs is quite low and that absorption of water by these trichomes is highly improbable. However, our suggestion of an overall high concentration of water in the adaxial cavity of the leaf, which serves to decrease the transpiration rate, is supported by these tests.

Cuticular ornamentation

Cuticular thickness may be affected by light, temperature, soil, atmospheric moisture and altitude (Wilkinson 1979). In *Passerina*, with many species adapted to the Cape Mediterranean climate, all members have a relatively thick cuticle, but it was the thickest in *P. comosa*, *P. glomerata*, *P. burchellii*, *P. galpinii* and *P. paleacea* (Table 2). The first two species grow in the northwestern parts of the Western Cape and on the mountains in and around the Little Karoo (= Karoo Mountain Centre *sensu* Weimarck 1941), areas with high light intensity, high temperature and low atmospheric moisture. *P. burchellii*, growing on high mountains at Villiersdorp and Genadendal, is exposed to high light intensity as well as high and low critical temperatures. *P. galpinii* grows on calcrete and *P. paleacea* is exposed to salt spray and wind. In *P. drakensbergensis*, *P. falcifolia*, *P. paludosa* and *P. sp. nov. 1*, the thickness of the CM is $\pm 20 \mu\text{m}$. Of these species, *P. falcifolia*, from the mountains between George and Uitenhage, and *P. drakensbergensis*, from high altitudes in the Bergville District of KwaZulu-Natal, are exposed to relatively high atmospheric moisture. However, it is difficult to speculate on the functional significance of the relatively thin cuticles in *P. paludosa*, from salt marshes in the Cape Peninsula, and *P. sp. nov. 1*, a species from Waboomberg, one of the highest points in the Western Cape and often covered by snow in winter.

FIGURE 5.—Abaxial leaf epidermis and structure of CM in *Passerina*. Epidermal macerations stained with safranin and t/s of epidermis stained with Sudan Black B. A–C, *P. drakensbergensis*, Bredenkamp 1018, 1019: A, cells arranged in rows with 9 or 10 globular papillae per cell; B, inner surface facing upwards, cells oblong in shape with 9 or 10 papillae per cell; C, CM layered, with cuticular layer and cuticle proper, also globular papillae. D–F, *Passerina* sp. nov. 1, Bredenkamp 1044, 1046: D, several domes per cell, CM irregularly marked by ice crystals; E, cells arranged in rows, oblong in shape with CM irregularly marked by ice crystals; F, geometrical plates, flat or slightly raised. G–I, *P. rigida*, Bredenkamp 1013, Ward 7211: G, cells arranged in rows, plates abundant; H, cells arranged in rows, isodiametric to slightly oblong; I, CM pronounced at junctions of epidermal cell walls, grooved in midline of joining walls, concavities and convexities not conspicuous. J–L, *P. paludosa*, Bredenkamp 1035, Thoday 100: J, cells arranged in rows, CM pronounced at junctions of epidermal cell walls, grooved in midline of joining walls, concavities and convexities conspicuous; K, cells arranged in rows, cells oblong; L, CM pronounced at junctions of epidermal cell walls, grooved in midline of joining walls. Abbreviations: cl, cuticular layer; co, concavity; cp, cuticle proper; cw, outer periclinal cell wall; cx, convexity; gr, groove in CM; pa, papillae; pe, cuticular peg; pl, plates. Scale bars: A, D, E, G, H, J–L, $100 \mu\text{m}$; B, C, F, I, $10 \mu\text{m}$.

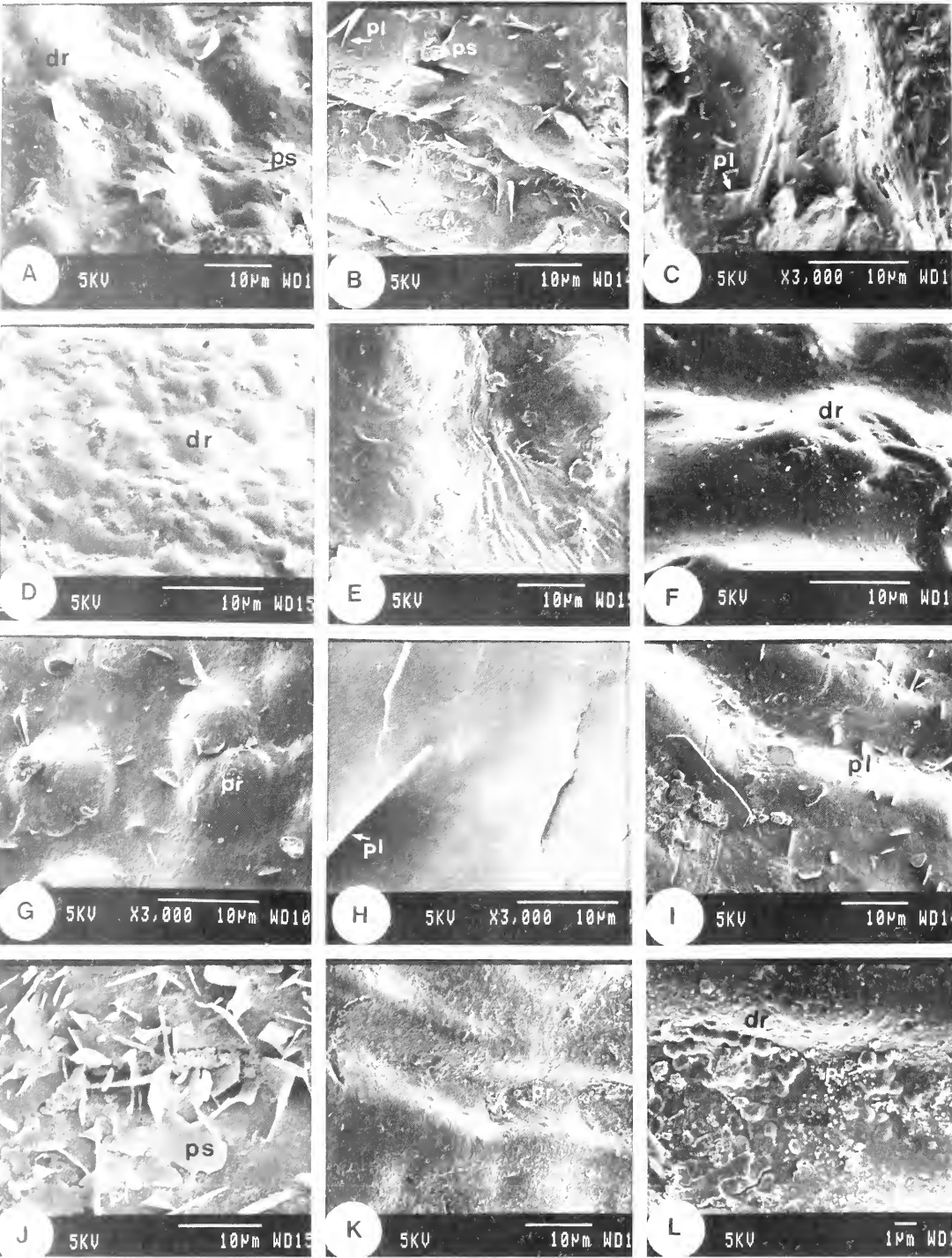


FIGURE 6 — SEM micrographs of abaxial leaf surfaces, the CM and epicuticular waxes in *Passerina*. A, B, *P. comosa*, MacDonaldd 2125: A, droplets present in epicuticular wax, platelets flaking from smooth wax coating, B, wax platelets flaking from smooth wax coating, plates present. C, *P. glomerata*, Bredenkamp 973, outer perichinal wall convex, plates scarce, square to oblong, raised 30°–90°; D, *P. ericoides*, Bredenkamp 956, droplets present in epicuticular wax; E, *P. obtusifolia*, Bredenkamp 929, smooth wax coating also covering domes. F, G, *P. burchellii*, Stokoe 2542: F, droplets at apices of domes; G, small round protrusions at apices of papillae. H, *P. filiformis*, Bredenkamp 1016, upright plates separate from surrounding wax, orientated at an angle to cell rows; I, *P. pendula*, Bredenkamp 908, plates frequent, perpendicular to cell rows, square to oblong, flat or raised; J, *P. rigida*, Bredenkamp 1013, platelets and plates; K, L, *P. paleacea*, Bredenkamp 961, wax droplets, protrusions and flat shapeless lumps contributing towards soft wax coating or smooth layer. Abbreviations: dr, droplets in epicuticular wax, pl, plates; pr, small round protrusions of epicuticular wax; ps, platelets. Scale bars: A–K, 10 μm; L, 1 μm.

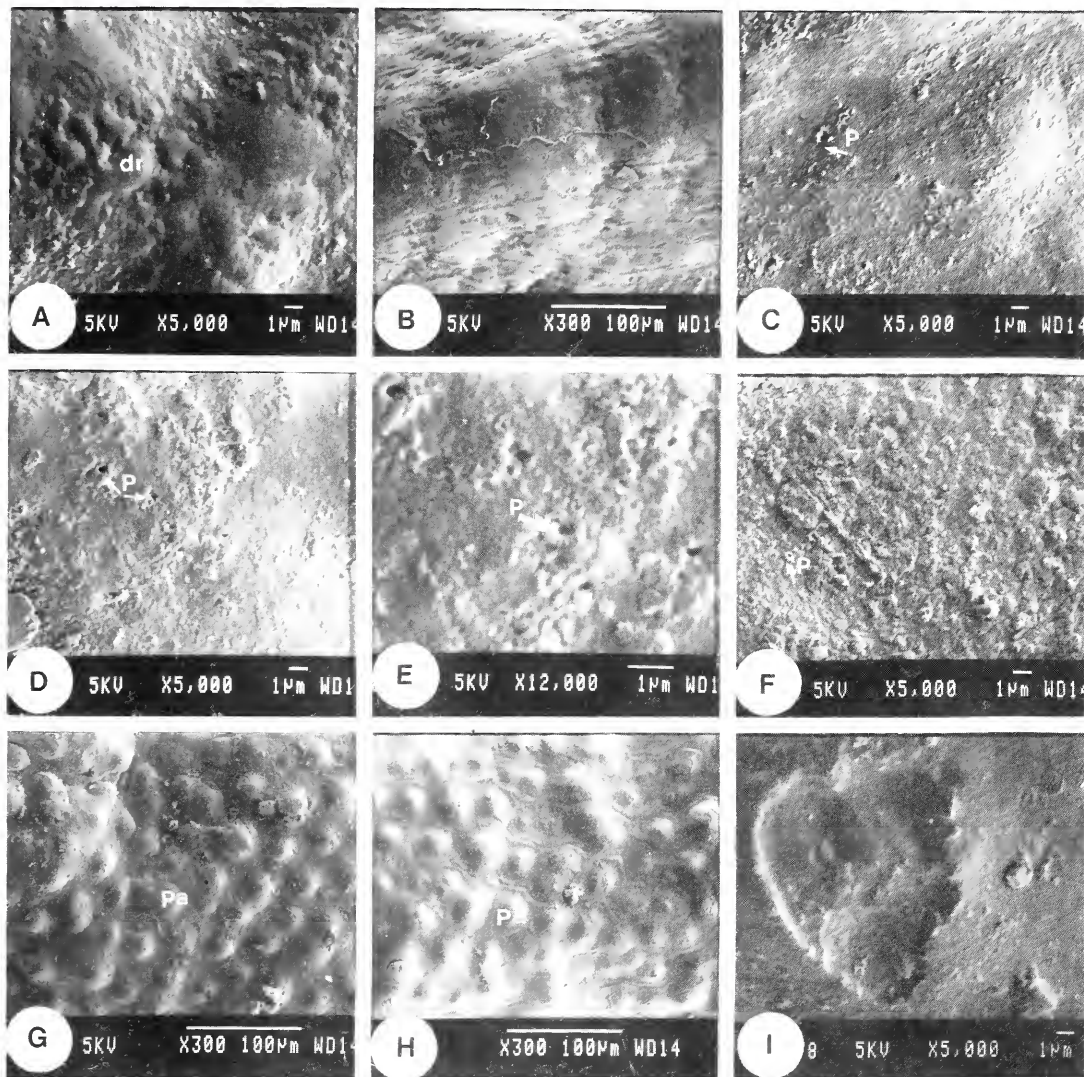


FIGURE 7.—SEM micrographs of abaxial leaf surfaces of *Passerina* washed in chloroform for one minute, compared to unwashed specimens. A–E, *P. paleacea*, Bredenkamp 961: A, unwashed leaf showing droplets in smooth wax coating; B, low magnification of washed leaf, showing CM devoid of epicuticular wax; C–E, higher magnifications showing pores in CM. F, *P. ericoides*, Bredenkamp 956, washed specimen showing pores in CM. G–I, *P. obtusifolia*, Bredenkamp 929: G, unwashed specimen; H, I, washed specimens showing corroded apices of papillae. Abbreviations: dr, droplets in epicuticular wax; p, pore; pa, papillae. Scale bars: A, C–F, I, 1 µm; B, G, H, 100 µm.

Haberlandt (1914), following a study of plants in tropical rain forests, considered the function of papillose epidermal cells as concentrating limited light by acting as lenses. Bredenkamp & Van Wyk (1999) speculate that, in *Passerina*, the convex outer periclinal epidermal cell wall may well focus light rays onto the mesophyll, whereas large vacuoles filled with phenols and the mucilage formed by the cellulose slimes (inner periclinal walls) protect the mesophyll from potentially dangerous UV-B radiation. According to Wilkinson (1979) the presence and prominence of papillae are diagnostically unreliable because they vary with the climate or distribution of the species; only morphologically distinct types can be used for diagnostic purposes. However, distinct epidermal cell papillae characterise *P. comosa*, *P. obtusifolia*, *P. burchellii*, *P. drakensbergensis* and *P. sp. nov.* 2

(Figures 4B–C, G–L; 5A–C). The presence of these papillae could have been induced by the high light intensity of the areas in which these plants grow.

Epicuticular waxes

In their study of the epicuticular waxes in the families of the Dilleniidae and Rosidae, Ditsch & Barthlott (1997) documented the numbers of genera, species and hybrids in which different wax types occur, without identifying the various taxa. The epicuticular waxes of 12 genera, 31 species and two hybrids were studied in the Thymelaeaceae. Of these, nine genera and 26 species have wax flakes, one species has angled platelets and four genera and five species have no crystalloids. Our

observations indicate that the simple plate-type waxes found in *Passerina* correspond well to those described by Ditsch & Barthlott (1997) in the Thymelaeaceae. Of the 17 species in *Passerina*, two have wax flakes, eight have platelets or angled plates and seven are devoid of crystalloids (Figure 6, Table 3).

The mechanism of wax extrusion through the cuticle is highly controversial (Baker 1974; Jeffree *et al.* 1975; Hallam 1982). Baker (1982) discusses the extrusion of wax by means of 'pores and channels, the liquid extrusion theory, polymerization theory and the crystallization theory'. Hallam (1982) proposes that wax or wax precursors in their protein or glycoprotein 'shells' move through the cuticle and burst on the surface, liberating the wax from the 'package'; on crystallization, the protein coats stick to the surface as the wax crystals develop.

Our results indicate small pores in the cleaned, de-waxed cuticle of *P. paleacea* and *P. ericoides* (Figure 7B–F), after washing leaves in chloroform. Both Baker (1982) and Hallam (1982) are convinced that detailed investigations by many investigators have failed to confirm the presence of pores or microchannels in certain plant cuticles and that pores have not been shown to connect with the plasmalemma of the epidermal cytoplasm below. Although the presence of pores has been confirmed by our study, further research on the ultrastructure of the CM in *Passerina* could be most informative.

Freeman *et al.* (1979), working on *Citrus*, found amorphous wax layers on immature leaves and fruit, with small protrusions and isolated regions of upright platelets developing, eventually followed by cracks and irregular plates. Similarly in *Passerina*, wax droplets, protrusions and flat, shapeless lumps contribute towards a soft wax coating or a smooth layer. Species of *Passerina* with soft wax coatings, without platelets or plates, are summarised in Table 3. In *P. comosa*, *P. filiformis* and *P. rigida* (Figure 6B, H, J) platelets and plates are formed as a result of cracks developing on the outer wax surface, crystallising into irregularly shaped flakes, which gradually become square or oblong with 'entire' or 'non-entire' margins, often becoming distinctly edged. In *P. filiformis* (Figure 6H) upright plates separate from the surrounding wax, orientating themselves at an angle to the cell rows, eventually resulting in most plates being arranged more or less perpendicularly to the cell rows. Wax type, as well as the presence or absence of plates and platelets, is apparently genetically determined (Baker 1982). For example, *P. ericoides*, *P. rigida* and *P. paleacea* (Figure 6D, J, K) all grow along the sea shore, where they are subjected to wind, salt spray and high light intensity, and yet, *P. ericoides* and *P. paleacea* have coverings of soft waxes only, whereas platelets and plates are abundantly present in *P. rigida*. However, in plate waxes the number of platelets and plates, size, configuration and distribution of the surface wax structures can be considered as environmentally induced (Baker 1974, 1982).

Functions of epicuticular waxes

Possible functions of epicuticular waxes are discussed by Jeffree (1986). In *Passerina*, large areas of the abaxi-

al epidermis are exposed to the atmosphere because the inverse-ericoid leaves are usually closely appressed to the stem. In response to the warm, dry summers of the Mediterranean climate of the Cape, it is proposed that the CM, including the abaxial epicuticular waxes, has a water-proofing function, protecting the leaves against desiccation and limiting transpiration to the adaxial epidermis only. As the leaves are decussately arranged, the water-repelling function of the waxes would cause droplets of water to run off the abaxial epidermis, into the concave, hairy adaxial surface of the lower leaf, resulting in a decreased transpiration rate owing to the higher adaxial water concentration. According to Jeffree (1986) the wettability of the plant surface is determined by its microroughness. The presence of crystalloid platelets and plates, and especially their arrangement perpendicular to cell rows, may facilitate the retention of moisture.

Systematic value

Epicuticular waxes have been proven taxonomically valuable, among others in the study of the Centrospirmae (Engel & Barthlott 1988), Dilleniidae and Rosidae, including the Thymelaeaceae (Ditsch & Barthlott 1997), at sectional level in *Eucalyptus* L'Hér. (Hallam & Chambers 1970) and at species level in *Hordeum* L. (Baum *et al.* 1989). In *Passerina* the presence or absence of crystalloid platelets or plates combined with characteristics of the CM and the outer periclinal cell walls of the abaxial epidermis, makes it possible to distinguish between two groups in the genus. This distinction is species-specific for most of the 17 species examined (Table 3).

Ecological aspects of leaf epidermis

The structure and function of the epidermis should be considered in context with gross leaf morphology and arrangement. Leaf arrangement is of vital importance to the physiology of the plant. The epidermis serves as an envelope, physically protecting the mesophyll, the largest part of the abaxial epidermis forming a multifunctional barrier to the environment. The thin adaxial epidermis is concealed in the groove of the cymbiform leaf in most cases; it is almost covered by dense, long, spiralised uniseriate trichomes and contains the stomata, which are often raised. This arrangement is likely to reduce the rate of transpiration, especially if moisture can be retained by the indumentum. The abaxial epidermis is probably multifunctional. The whole of the CM has a waterproofing function and the epicuticular waxes also have a water-repelling function. At the same time the CM may play a major part in focusing light rays onto the palisade parenchyma. Large tanniferous vacuoles may play a role in the possible absorption of UV-B radiation, and mucilage formed by the cellulose slimes (inner periclinal walls) possibly protects the mesophyll from desiccation (Bredenkamp & Van Wyk 1999).

The expansion and inrolling of the leaf margins in *Passerina*, as a result of changing turgor pressure in the epidermal cells, were described by Thoday (1921). He regards the main mechanism involved as the co-ordina-

tion between the turgor pressure and the difference in size and thickness of cell walls of the ad- and abaxial epidermis, whereas the plicate anticlinal cell walls of the abaxial epidermis protect the cells against bending stress. Stomata (or at least the indumentum) are exposed when the leaf margins expand and are protected in a villous groove when the leaf margins are rolled inwards, thus regulating the rate of transpiration.

CONCLUSIONS

Leaf shape and structure in Thymelaeaceae exhibit a transformation series from mainly dorsiventral, the prevailing family feature, to isobilateral or centric in *Diarrhodon* Turcz., *Pimelea* Banks & Soland. and *Thymelaea* Juss. (Metcalf & Chalk 1950). All the mentioned states are present in *Lachnaea* and *Cryptadenia* (Beyers 1992) and, as the most advanced state, inversely dorsiventral leaves in *Passerina*. A transformation series can also be illustrated by the presence of amphistomatic, hypostomatic and epistomatic leaves in the Thymelaeaceae (Metcalf & Chalk 1950), the epistomatic state in *Passerina* considered to be the most advanced (the collateral vascular bundles of the leaves, with xylem arranged adaxially and phloem abaxially, rule out the possibility of resupination of the leaves).

The most pronounced epidermal characters of the Thymelaeaceae are anomocytic stomata (Metcalf & Chalk 1950), unicellular trichomes and mucilagination of epidermal cells. In the present study the presence or absence, distribution of or changes in the above-mentioned structures, were used as distinguishing characters at both generic and species levels. Mucilagination of epidermal cells is often found both ad- and abaxially in the leaves of Thymelaeaceae. In *Passerina*, mucilagination takes place in the abaxial epidermis only. At species level the sunken stomata and stomatal crypts of *Passerina* sp. nov. 1 are used in the delineation of the new taxon and *P. comosa* is distinguished by the presence of unicellular trichomes on the abaxial surface of the leaves.

On the basis of abaxial cuticular characters, it has been possible to distinguish two groups of species in the genus. Group A comprises *P. burchellii* Thoday, *P. comosa* C.H.Wright, *P. ericoides* L., *P. glomerata* Thunb. and *P. obtusifolia* Thoday. Group B comprises *P. drakensbergensis* Hilliard & B.L.Burt, *P. falcifolia* C.H.Wright, *P. filiformis* L., *P. galpinii* C.H.Wright, *P. montana* Thoday, *P. paleacea* Wikstr., *P. paludosa* Thoday, *P. pendula* Eckl. & Zeyh., *P. rigida* Wikstr., *P. rubra* C.H.Wright, *P. vulgaris* Thoday, *P. sp. nov. 1*, *P. sp. nov. 2*, *P. sp. nov. 3* and *P. sp. nov. 4*. Certain species in each of the two groups seem to be naturally allied. Distribution patterns of *P. obtusifolia* and *P. glomerata* coincide at Worcester and transitional types can be clearly distinguished. Transitional types are similarly present in *P. filiformis* and *P. vulgaris* in the Cape Peninsula and in *P. filiformis* and *P. falcifolia* near Knysna.

Hence it can be concluded that the conspicuous differences as well as the concise characters of the ad- and abaxial epidermis, critically described and discussed in this paper, can be used as taxonomic tools at the family,

genus and species levels. Furthermore, the leaf epidermis in *Passerina* is probably most valuable to the plant in terms of ecological adaptation, considering the wide distribution of the genus in southern Africa as well as the accompanying geographical and climatic variation. The gross leaf morphology and the ad- and abaxial epidermal characters have been most useful in the interpretation of the possible functioning of the leaves and are of vital importance in the survival strategies of the plant.

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Vegetation of the coastal fynbos and rocky headlands south of George, South Africa

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Keywords: gradient analysis, numerical syntaxonomy, ordination, phytogeography, phytosociology

ABSTRACT

Community structure and composition of the coastal fynbos and rocky headland plant communities south of George, southern Cape, were studied. Vegetation was analysed using standard sampling procedures of the floristic-sociological approach of Braun-Blanquet. The relevé data were subject to TWINSpan-based divisive classification, and ordinated by Principal Coordinates Analysis with the aim to identify vegetation coenocline subsequently interpreted in terms of underlying environmental gradients. Most of the sampled vegetation was classified as coastal fynbos. The *Leucadendron salignum*–*Tetralix cuspidata* Fynbos Community was found to occupy sheltered habitats, whereas the *Relbunium calycinum*–*Passerina vulgaris* Fynbos Community was found in exposed habitats. The other two communities characterise strongly exposed rocky headlands. The *Pterocelastrus tricuspidatus*–*Ruschia tenella* Community is wind-sheared scrub, and the *Gazania rigens*–*Limonium scabrum* Rocky Headland Community is a loose-canopy, low-grown herbland, characterised by the occurrence of partly salt-tolerant and succulent herbs. The ordination of the fynbos communities revealed a horseshoe structure allowing a direct recognition of a coenocline spanning two fynbos communities along the Axis 1 interpreted in terms of exposure to wind and salt spray. A considerable amount of alien plant infestation was also present. This appears to be the largest threat to the continued existence of this coastal fynbos.

INTRODUCTION

Fynbos occurring in close vicinity of the coast has been studied in detail in many regions of South Africa (Boucher 1977; Van der Merwe 1979; Cowling 1984; Taylor 1985; Hellström 1990; Taylor & Boucher 1993; Hoare 1994). There are, however, still many portions of the coastline, especially outside formal reserves, which remain only poorly known. Only 79 km of the central south coast falls into existing protected areas, namely the Goukamma Nature Reserve, the Robberg Nature Reserve and the Tsitsikamma Coastal National Park (Jarman 1986). The promulgation of the Agulhas National Park may alter these statistics (World Wide Fund for Nature 1999).

The area along the coast south of George, the present study area, is of interest because of its scenic beauty and its location in the centre of the popular Garden Route. Interest in coastal development for recreational purposes throughout the Garden Route is likely to impact on areas which have not yet been encroached upon. The extent of vegetation cover outside formally protected areas has been considerably transformed, and of the remaining natural areas large portions have been invaded by alien species. It was therefore suggested by Cape Nature Conservation (George) that a detailed study be undertaken along the coast south of George to provide information on the local vegetation and flora and possible importance of the study area for conservation (G. Hellström pers. comm.). This particular study features descriptions of the plant communities of habitats close to the coastline.

STUDY AREA

The study area extended from Rooiklip, SE of Pacaltsdorp, to Ghanwabaai, 3 km E of Glentana (Figure 1), and covered ± 190 hectares. Glentana, and the area west of it, has been extensively developed and was therefore found unsuitable for the intended study. The fynbos vegetation in the study area has been classified as Asteraceous Fynbos by Cowling & Holmes (1992) and it was broadly classified by Acocks (1988) as ‘cultivated land, plantations, dense alien communities and open sandy areas’, a description which gives a clear indication of the transformed state of the vegetation. The vegetation of the coastline area is classified as Dune Thicket (Low & Rebelo 1996), which forms a mosaic with Dune Fynbos (Low & Rebelo 1996) in the region including the study area.

The coastline consists of steep coastal cliffs ranging in height from 50 to 70 metres, forming rocky headlands. The plenitude of alternating bays and headlands has resulted in microhabitats with varying degrees of exposure to the prevailing winds, salt spray and sun. Coastal soils vary markedly according to substrate, but are often calcareous and coarse-grained. Topography is the dominant factor affecting soil formation and the removal of the products of weathering may exceed their formation, especially on slopes. The coastal cliffs of the study area are Rooiklip Granite-Gneiss of the Kaaimans Group and are pre-Cape intrusive granite rocks (South African Committee for Stratigraphy 1980). These rocks are important because, upon weathering, they form base-rich substrates containing exchangeable cations that are important for soil formation and plant nutrient cycling (Deacon *et al.* 1992).

The Köppen’s climate classification code for the George coastal area is Cfb, which indicates warm, temperate climate (Schulze & McGee 1978). The mean annual temperature is $\pm 17^{\circ}\text{C}$, with a mean temperature range

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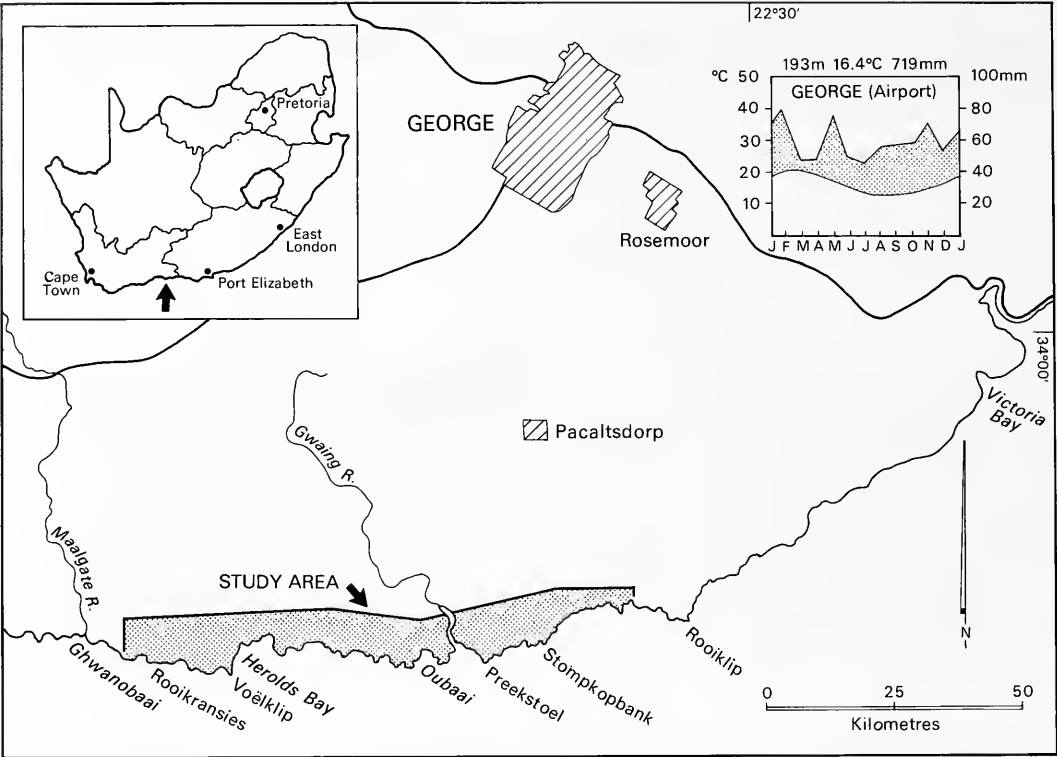


FIGURE 1.—Map of the study area and climate diagram for George.

of 8°C near the coast. The area has precipitation during all months of the year, with three prominent peaks in spring, summer and autumn, although there is no precipitation deficit at any time of the year (Figure 1). Sea mists may provide additional moisture on seaward-facing slopes. Pronounced strong winds blow along the entire coastal belt, varying in direction according to location and season. In the study area, wind from the southwest and west were found to be more important, since their frequency was higher (Weather Bureau 1994). Wind velocity has been found to be important in coastal plant communities, since the greater the velocity of the wind, the higher the salt load of the moving air, which may have a serious detrimental effect on the growth of plants (Avis & Lubke 1985). Importance values (Table 1) were determined which took into account the velocity and frequency of winds from different directions (IV = mean monthly direction frequency multiplied by mean monthly velocity expressed as percentage of total of all values for year). Westerly winds had the highest importance values throughout the year but were of greatest importance during the winter months. Southwesterlies showed a similar pattern. Easterlies and southeasterlies had the second highest importance values, but these were most prevalent during spring and summer (September to March).

MATERIAL AND METHODS

Aerial photographs were used to stratify the region into broad vegetation complexes based on vegetation structure and relevés (25 m² each) were made within

these zones. The quadrat size was determined from species/area curves drawn from data collected in the study area, but also conformed to a scale-related approach to vegetation sampling, i.e. the size of the relevé was related to the scale at which the vegetation was studied (Rutherford & Westfall 1994). Riparian thicket, dune thicket, dense alien stands and agricultural lands were not sampled. Standard field techniques and the 7-grade sampling scale of Braun-Blanquet (Westhoff & Van der Maarel 1973; Werger 1974) were used to record the cover/abundance values for each vascular species encountered in the relevés. Topographic information, including slope, aspect and altitude were also

TABLE 1.—Importance values of winds from different directions in the months of the year. Bold text shows cells with importance values greater than 1. (IV's calculated from data from Weather Bureau. See text for method)

Month	N	NE	E	SE	S	SW	W	NW
J	0.01	0.07	2.6	2.3	1.7	1.8	1.1	0.3
F	0	0.1	2.8	1.8	1.6	1.4	1.0	0.4
M	0.03	0.04	1.7	1.6	1.2	1.1	1.0	0.3
A	0.08	0.04	0.8	1.0	0.9	1.0	1.6	0.8
M	0.35	0.08	0.5	0.5	0.5	1.0	3.5	2.1
J	0.48	0.05	0.4	0.3	0.4	0.7	2.7	2.7
J	0.39	0.1	0.5	0.5	0.5	0.7	2.5	2.0
A	0.38	0.1	0.9	0.8	0.8	1.0	2.5	1.5
S	0.24	0.1	1.2	1.3	0.9	1.3	2.3	0.9
O	0.10	0.06	2.3	1.6	1.2	2.0	1.8	0.7
N	0.03	0.02	2.9	2.0	1.6	1.7	1.5	0.4
D	0.01	0.05	2.3	2.2	1.7	1.8	1.5	0.3
TOTAL	2.1	0.8	18.9	15.9	13.0	15.5	23.0	12.4

recorded. Physical soil properties, such as pH, conductivity, organic matter content, water-holding capacity, as well as the relative fraction of coarse, medium and fine sand, silt and clay, were ascertained in a subset of 20 relevés. The general methodology used by the US Department of Agriculture (USDA 1972) was followed for analysing soils.

The vegetation data were initially classified using TWINSpan (Hill 1979), producing a rough species-by-relevé matrix, which was further rearranged in order to finely tune the relevé/species coincidence patterns supposed to carry meaningful ecological information. The data from only the fynbos communities were subject to ordination by Principal Coordinates Analysis based on similarity ratio as resemblance measure with no *a priori* data transformation using the programme package SYN-TAX-5 (Podani 1993, 1994).

For the descriptions of vegetation communities, three informal ranks of vegetation units are recognised: community, subcommunity, and facies. Facies (Braun-Blanquet 1964) represents the lowest-ranked unit and corresponds to vegetation stands dominated by a single species, mostly an alien element.

RESULTS AND DISCUSSION

Classification of plant communities

The rearranged species-quadrat matrix (Table 2) revealed two groups of plant communities: the majority of the relevés were classified as coastal fynbos (Communities A & B) and the remainder of the relevés as (non-fynbos) rocky headland communities (Communities C & D). A summary of the community environmental and floristic relationships is given in Figure 2. The following communities, subcommunities and facies were identified:

A. *Leucadendron salignum*–*Syncarpha paniculata* Fynbos Community

This community occurs in areas that are protected from coastal winds either by headlands or the proximity of coastal thicket (Figure 3) and has a different species composition to the fynbos on the exposed summit of the coastal cliffs. Diagnostic species: *Leucadendron salignum*, *Aspalathus asparagoides*, *Hermannia angularis*, *Metalasia acuta*, *Helichrysum cymosum* and *Bobartia aphylla*. Dominant species: *Syncarpha paniculata* and *Passerina vulgaris*. Common species: *Tetraria cuspidata*, *Cliffortia falcata*, *Metalasia pungens*, *Lobelia tomentosa*, *Erica discolor* and *Phyllica confusa*. Many stands of this community have been seriously invaded by the alien species *Acacia cyclops*, *Leptospermum laevigatum* and *Pinus* spp.

Slopes vary from moderate to steep and soils are generally deeper and finer-grained than on cliff summits. There is high species richness (19 species on average) in this community. The habitat is more variable than on the cliff summits, thus leading to a greater species turnover between localities. The geographic distribution of this

community beyond the present study area is unknown. Four subcommunities are recognised and described.

Aa. *Thamnochortus cinereus* Subcommunity

Diagnostic species: *Thamnochortus cinereus*, *Polygala microlopha* and *Cliffortia* sp. (Victor 313). It is situated below a housing development at Herold's Bay Extension; there was no evidence of recent fire and the subcommunity is possibly one form of a fire-climax vegetation in protected areas.

Ab. *Protea neriifolia* Subcommunity

Diagnostic species: *Protea neriifolia*. It has developed in the absence of fire and is possibly a fire-climax vegetation of protected areas. *Bobartia aphylla* and *Pelargonium fruticosum* serve as common linking species to subcommunities Aa and Ab.

Ac. Typical Subcommunity

Lacks the diagnostic species of the other three subcommunities, but contains the diagnostic species of the *Leucadendron salignum*–*Syncarpha paniculata* Fynbos Community. There was evidence of recent fires in a number of the relevés.

Ad. *Hermannia althaeifolia* Subcommunity

Diagnostic species: *Hermannia althaeifolia*, *Hibiscus aethiopicus*, *Ficinia albicans* and *Ursinia saxatilis* as well as a number of infrequently occurring species (Table 2). Most of the relevés had evidence of being burnt recently, suggesting that it is an early post-fire successional stage.

The vegetation height varies from 1 m, where dwarf shrubs are dominant, to over 2.5 m where shrubs of the exotic *Leptospermum laevigatum* are found. The mean species richness of this subcommunity is 20 species on average, but this may be reduced to only eight species where invasion by exotic shrubs has taken place, as is the case of the *Acacia meamsii* facies (Table 2, rel. 23).

B. *Relhania calycina*–*Phyllica confusa* Fynbos Community

This community makes up the greatest proportion of the fynbos in the study area and also extends beyond the boundaries of the present study area along the summit of the coastal cliffs towards Knysna (Figure 3). Diagnostic species: *Relhania calycina* subsp. *calycina* and *Viscum capensis*. Dominant species: *Erica discolor*, *Phyllica confusa*, *Passerina vulgaris* and *Tetraria cuspidata*. Common species: *Thesium virgatum*, *Agathosma ovata*, *Erica peltata*, *Syncarpha paniculata* and *Cliffortia serpyllifolia*.

The dwarf shrub layer of this community is usually about 1 m in height and the herb layer about 0.4 m. The total cover of the vegetation is slightly lower than for

TABLE 2.—Classification of the vegetation of the coastal cliff habitats south of George, South Africa

Key to communities and subcommunities:

- A: *Leucadendron salignum*–*Syncarpha paniculata* Fynbos Community
 - Aa: *Thamnochortus cinereus* Subcommunity
 - Ab: *Protea neriifolia* Subcommunity
 - Ac: Typical Subcommunity
 - Ad: *Hermannia althaeifolia* Subcommunity
 - F: *Acacia mearnsii* facies
- B: *Relhania calycina*–*Phyllica confusa* Fynbos Community
 - Ba: *Tetraria cuspidata* Subcommunity
 - Bb: *Eriocephalus africanus* Subcommunity
- C: *Pterocelastrus tricuspidatus*–*Ruschia tenella* Coastal Scrub Community
 - S: *Sporobolus virginicus* facies
- D: *Gazania rigens*–*Limonium scabrum* Rocky Headland Community
 - G: *Gazania rigens* facies

Legend to vegetation layers: hl, herb layer; jl, juvenile woody species; sl, upper shrub layer; s2, low shrub layer; t3, low tree layer. Taxonomic notes, *Gazania rigens* = *Gazania rigens* var. *uniflora*; *Limonium scabrum* agg. is a new taxon pending formal description (L. Mucina, in prep.) and is closely related to *L. scabrum* (Thunb.) Kuntze; *Drosanthemum marinum* agg. is a complex of *D. marinum* and *D. delicatulum* and might represent one taxon after a revision (P. Burgoyne pers. comm.).

Relevé number	11 11111111222 2	222223333333333444 4444444555	555555566 6	66666 6
	12 34567 8901 23456789012 3	4567890123456789012 3456789012	345678901 2	34567 8
Community	AA AAAA AAAA AAAAAAAAAA A	BBBBBBBBBBBBBBBBBBBB BBBBBBBBBB	CCCCCCCC C	DDDD D
Subcommunity	aa bbbb cccc ddddddddd d	aaaaaaaaaaaaaaaaaaaa bbbbbbbbb		
Facies	F		S	G
Aspect (degrees)	22 2221 2112 2112111211 1	1122111211122211121 2212 1111	122221213 1	12222 2
	42 99998 0881 28948382888 7	8870883788820088808 2780968585	292028086 8	84422 1
	05 33330 3004 50080505000 5	0003005000053300030 5003080808	030350300 0	08850 0
Slope (degrees)	22 33221 1 11 2 1 1	2 111 2 1 43 1 1	23151 431	43332 3
	23 00066 3545 33228685776 7	8020133899994065058 9005841918	008025552 2	02005 6
Altitude (metres)	1 1 1	1		
	66 34660 6451 09969996999 9	5547784344541693989 4284146665	254331313 2	11144 4
	50 55000 0055 05000000000 0	0050005005000000005 0005550000	550555000 5	24800 5
Number of species	21 12211 1122 2112212211 2	21121212111111122 2 1221111112	1 11 111	1 1
	23 70345 8665 35673607760 8	4835917364356990170 2343596052	054078297 8	46073 1

Coastal Fynbos

<i>Tetraria cuspidata</i>	-hl	ar rrr.a +.+. .a+.+.rr+ r	++3b1+.a3b+a..maba b....+.a
<i>Thesium virgatum</i>	-s2	.. rrr.. ..+++	++++.+++++.+.+.r r+++++.+r.. .
<i>Syncarpha paniculata</i>	-hl	.. 33a.r .33b .rb+la+bb+ .	++a+++++1++++.a.a r+.+.+.+
<i>Erica formosa</i>	-s2	3b 4.... 3.a..... .	+.a.a
<i>Cliffortia falcata</i>	-s1 rrr a++ .a.++++.aa . .	++.....m.....
<i>Metalasia pungens</i>	-s2rra .a.a .+.+aa aa . .	+.+.+.+.+.+.r.....
<i>Erica peltata</i>	-s2+. .a.4+3b3bba b	++.3a++a++....aa . .++.+a+a
<i>Schizaea pectinata</i>	-hl	rr rr..r +.+. .+.+.+.+.+.+.r.r
<i>Restio triticeus</i>	-hl	.a .raaa +.+. 43...+.+.+. .	.3.+.+.+.r.r
<i>Lobelia tomentosa</i>	-hl	r. rr... r+.+. r...+arrr. r	+.+.r.....r.....
<i>Centella virgata</i>	-hl	r. ba...+.+. .	+.
<i>Pentstemon eriostoma</i>	-hla3l..3.a..+. .	+.r.....a.a.r .3...l...3
<i>Ficinia nigrescens</i>	-hl	.. rrrrr ++++.r.r+.+.r.....
<i>Carissa edulis</i>	-s2ab.. rrr+.+. +.+.r.....
<i>Aspalathus alopecurus</i>	-s2b... .a+.+.+.+.r.....+.+.r.....
<i>Anthospermum prostratum</i>	-hlr .++. a+.+.+.aa+.+.+.+.+.+.r.....
<i>Cullumia bisulca</i>	-hlr .++. .a+.+.+.r.r . .	+.r.....+.r.....
<i>Aspalathus florifera</i>	-s2+.+.b. .	..r.....m.....
<i>Falkia repens</i>	-hlr .+.+.+.+.+. .	+.+.+.+.+.r.....
<i>Crassula subulata</i>	-hlrr..+.+. +.r.r
<i>Disparago kraussii</i>	-hlr .+.+.+.+. .	+.
<i>Erica ericoides</i>	-s2r .+.+.+. .	+.+.+.r.....
<i>Rhus lucida</i>	-s2r .+.+.+. .	..r.....r.....+.
<i>Wahlenbergia desmantha</i>	-hlr.....+.+. +.

Leucadendron salignum–*Syncarpha paniculata* Fynbos Community

<i>Leucadendron salignum</i>	-s2	ba .ar.b l... r3ra..+.b.. .	aa.....b
<i>Aspalathus asparagoides</i>	-s2	aa .a.. +a.. .+.+.+.al.....
<i>Hermannia angularis</i>	-hl	.. rrr.. +.r+.+++rr+ r
<i>Metalasia acuta</i>	-s2+.+.a+b
<i>Helichrysum cymosum</i>	-hlr.. .r .+.+.+.r.....
<i>Bobartia aphylla</i>	-hl	a .arar .b..
<i>Pelargonium fruticosum</i>	-hl	. b bba.r .r

Thamnochortus cinereus Subcommunity

[illegible]

Protea neriifolia Subcommunity

Protea neriifolia -s2 |.. **br3.b**|.....|..|..+......r....|.....|.....|..|.....|

Hermannia althaeifolia Subcommunity

<i>Hermannia althaeifolia</i>	-hl+.++rr+	+	
<i>Hibiscus aethiopicus</i>	-hl	++.+...+.+	
<i>Ursinia saxatilis</i>	-hl+r...rrr.		r.
<i>Ficinia albicans</i>	-hl	aa...+.+	
<i>Clusia alaternoides</i>	-s2	r.	. .	++.+...+.+		r.
<i>Relbania pungens</i>	-s2	+..+...+.+	
<i>Chrysanthemoides monilifera</i>	-s2+...a.+	
<i>Diospyros lycioides</i>	-s2	+...+...b			a	. .	.
<i>Aspalathus kougaensis</i>	-s2aa.	
<i>Tritoniopsis antholyza</i>	-hl	r.+.+.+.+	
<i>Gerbera serrata</i>	-hl	r.b...+.+	
<i>Ficinia quinquangularis</i>	-hl+.+	
<i>Ischyrolepis triflora</i>	-hl+.+	
<i>Themeda triandra</i>	-hl+.3	
<i>Acacia mearnsii facies</i>														
<i>Acacia mearnsii</i>	-t3	b		b
<i>Leptospermum laevigatum</i>	-t3	b		b

Relhania calycina–*Plylica confusa* Fynbos Community

<i>Relbunium calycinum</i>	-hl	.. rr.r ..+	..	m+++a1maaab+++a+a b++++++1+
<i>Viscum capense</i>	-hl	.. r .. +.	..	+..+.+++++++r.r r
<i>Helichrysum teretifolium</i>	-hl
<i>Cassytha ciliolata</i>	-hl
<i>Carpobrotus edulis</i>	-hl
<i>Stoebe microphylla</i>	-hl	.. r	+
<i>Secamone alpini</i>	-hl	+
<i>Tetraria robusta</i>	-hl	b.r
<i>Tetraria compressa</i>	-hl	3

Eriocephalus africanus Subcommunity

Eriocephalus africanus -s2 |. r . | r | + . + . + . + | **b+b+a+aaal** | b.3 . r.3 . | |
Ficinia repens -hl |. | | | + + | + + | |

***Ruschia tenella*–*Gazania rigens* Coastal Rocky Headland Community**

[illegible]

***Pterocelastrus tricuspidatus*–*Ruschia tenella* Coastal Scrub Community**

	Pterocelastrus tricuspidatus	Sideroxylon inerme	Delosperma edwardsiae	Cineraria britteniae
-s2r r.r+. ra...a.l	bb45..+.	..r..b.
-hlr a.b.	..a.b.
-hlr r...+.	..r...+

Other native spp. common to coastal fynbos and rocky headland habitats

[illegible]

Invasive alien spp.

<i>Acacia cyclops</i>	-s2r3. rr++ r.r.a..ra.+	..+r.3ra.a33b+++ab.. a+4+..+b+.	3....br+r 3
<i>Acacia cyclops</i>	-j1	+.....
<i>Pinus pinaster</i>	-t1r.. r..r..f..	r..rrr.....f..
<i>Pinus pinaster</i>	-j1	r.....f..
<i>Leptospermum laevigatum</i>	-s2 +r+..r.b.
<i>Casuarina sp.</i>	-s2a..
<i>Leptospermum laevigatum</i>	-s1rf.....
<i>Acacia mearnsii</i>	-s1r.....
<i>Hakea sericea</i>	-s2r.f..a

TABLE 2.—Classification of the vegetation of the coastal cliff habitats south of George, South Africa (cont.)

Infrequently occurring spp. (sp. name; vegetation layer; relevé number(s), cover/abundance score)	
<i>Adromischus caryophyllaceus</i>	-h1: 48,+
<i>Agathosma capensis</i>	-s2: 1,r
<i>Amphithalea fourcadei</i>	-h1: 4,r; 24,+
<i>Anthospermum littoreum</i>	-h1: 67,+
<i>Aspalathus nigra</i>	-h1: 22,+
<i>Bassia diffusa</i>	-h1: 66,+
<i>Cassine papillosa</i>	-s2: 56,+; 59,+
<i>Cineraria geifolia</i>	-h1: 28,r
<i>Cineraria saxifraga</i>	-h1: 60,+
<i>Commelina africana</i>	-h1: 5,r
<i>Cotyledon orbiculata</i>	-h1: 58,r
<i>Crassula expansa</i>	-h1: 28,r; 47,+
<i>Crassula fascicularis</i>	-h1: 28,r
<i>Crassula rupestris</i>	-h1: 44,r; 48,+
<i>Crassula tetragona</i>	-h1: 67,+
<i>Cynodon dactylon</i>	-h1: 58,+
<i>Delosperma litorale</i>	-h1: 57,r
<i>Disperis capensis</i>	-h1: 14,r
<i>Disphyma crassifolium</i>	-h1: 11,+
<i>Drosera</i> sp. (Victor 318)	-h1: 1,r
<i>Ehrharta capensis</i>	-h1: 18,r
<i>Ehrharta erecta</i>	-h1: 45,+; 56,r; 59,r
<i>Eragrostis capensis</i>	-h1: 27,r
<i>Erica hispidula</i>	-h1: 3,r; 5,r
<i>Erica versicolor</i>	-s2: 12,r; 47,r
<i>Euchaetis albertiniana</i>	-h1: 37,+; 51,+
<i>Euclea crispa</i>	-s2: 16,+
<i>Ficinia gracilis</i>	-h1: 1,r
<i>Freesia alba</i>	-h1: 83,+
<i>Herschelianthe hians</i>	-h1: 41,+
<i>Hermannia salvifolia</i>	-h1: 13,+; 24,+
<i>Ischyrolepis helenae</i>	-h1: 3,r
<i>Knowltonia vesicatoria</i>	-h1: 12,+
<i>Lampranthus</i> sp. (Victor 220)	-h1: 57,r
<i>Lampranthus conspicuus</i>	-h1: 15,+
<i>Lobelia bicolor</i>	-h1: 56,r
<i>Myrica quercifolia</i>	-h1: 27,r
<i>Ornithogalum</i> sp.	-h1: 66,+; 67,+
<i>Phyllica strigulosa</i>	-s2: 8,+; 29,+; 46,+
<i>Plecostachys serpyllifolia</i>	-h1: 29,r
<i>Rhus crenata</i>	-s2: 56,+; 58,r
<i>Rhus glauca</i>	-s2: 37,+; 45,r; 58,+
<i>Rhynchosia capensis</i>	-h1: 1,r
<i>Rhynchosia ciliata</i>	-h1: 22,+
<i>Sarcostemma viminale</i>	-s2: 58,+
<i>Sutera aethiopica</i>	-h1: 45,r
<i>Syncarpha canescens</i>	-h1: 25,+
<i>Tarchonanthus camphoratus</i>	-s1: 12,+
<i>Tarchonanthus camphoratus</i>	-s2: 44,r
<i>Thesium lisae-mariae</i>	-h1: 1,r
<i>Tribolium uniola</i>	-h1: 31,+
<i>Vicia sativa</i>	-h1: 44,+

other fynbos communities in the study area, mostly due to an absence of a distinct restioid stratum. The community is exposed to sun and wind and is consequently hot and dry. Compounding this dryness, the soils are generally shallow and stony due to natural surface erosion at the summit of these cliffs. Slopes vary from flat to moderate. The community tends to grade into thicket inland, often with a tall *Passerina* belt before the true thicket. There is a high degree of invasion by *Acacia cyclops* (present in 78% of relevés), possibly causing habitat modification, which could ultimately lead to irreversible changes in species composition and vegetation structure.

Ba. *Tetraria cuspidata* Subcommunity

This subcommunity has the same dominant and common species as the Community itself, but with *Viscum capense* as a common species. It is usually found more inland of the other subcommunity suggesting that the two subcommunities form a gradient from lower altitude to wind-protected inland plant communities.

Bb. *Eriocephalus africanus* Subcommunity

Transition to lower altitude, steep-slope communities. It has slightly steeper slopes than the typical cliff summit community and is often moderately exposed to the influence of salt spray. There are also higher soil conductivity levels, which can be attributed to higher levels of wind-borne salt effects (see below). *Pterocelastrus tricuspidatus* and *Lampranthus sociorum* are occasionally present. This community is further marked by the absence of: *Tetraria cuspidata*, *Viscum capense* and *Syncarpha paniculata*.

C. *Pterocelastrus tricuspidatus*–*Ruschia tenella* Coastal Scrub Community

The woody component of this community reflects the species composition of the coastal scrub in the deeply incised valleys along this coastline and there is possibly a floristic gradient from this community into thicket on other steep slopes. Diagnostic species: *Pterocelastrus tricuspidatus* as well as infrequent occurrence of *Sideroxylon inerme*, *Delosperma edwardsiae* and *Cineraria britteniae*.

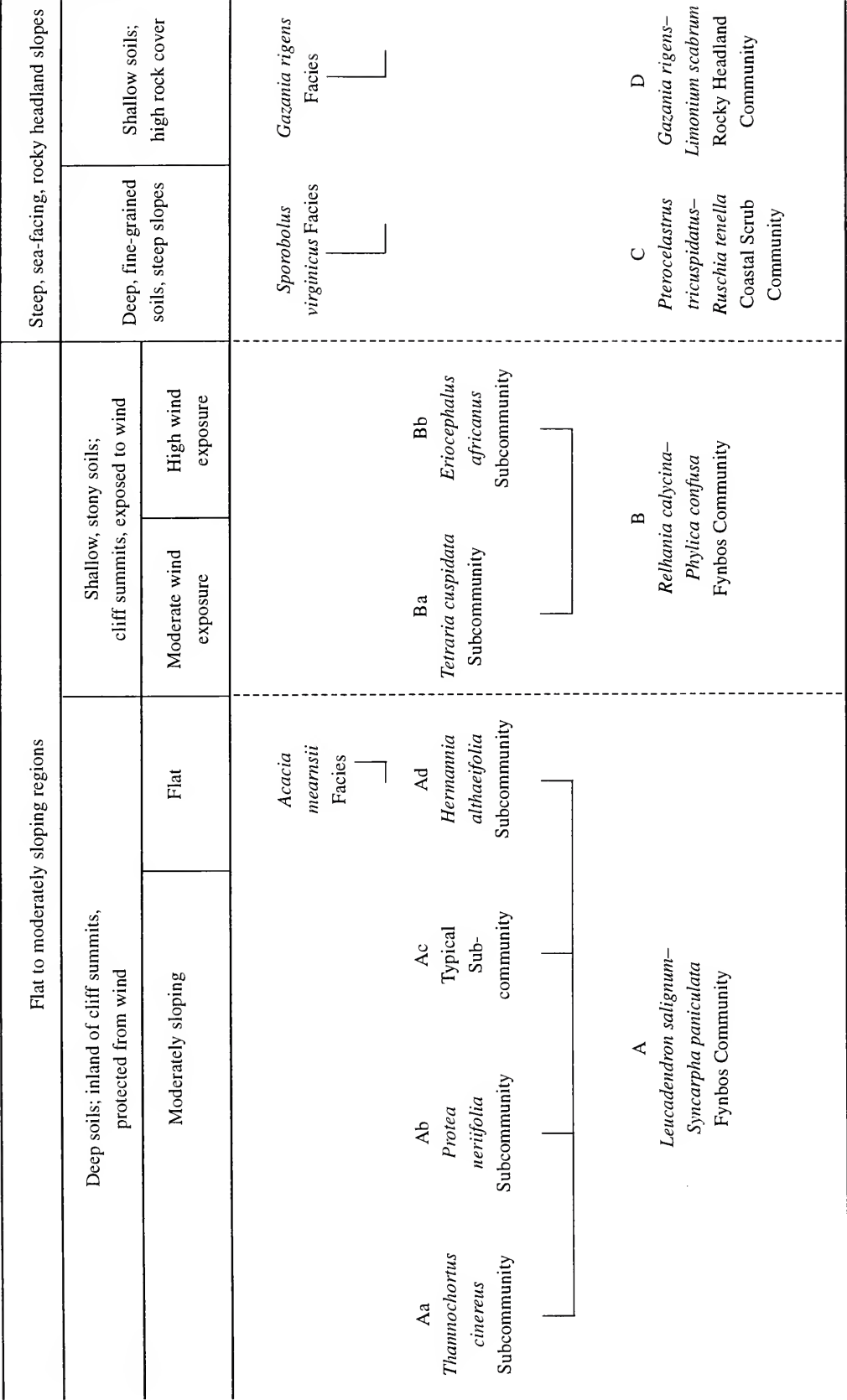


FIGURE 2.—Community environmental and floristic relationships in the coastal fynbos between Rooklip and Ghwanobaa, south of George, South Africa.

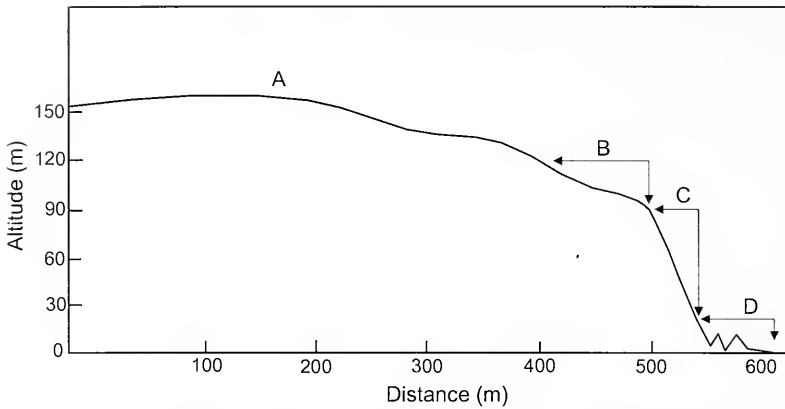


FIGURE 3.—Generalised profile diagram of coastal area south of George indicating the spatial relationship of communities to one another and the sea.

Common or dominant species: *Passerina vulgaris*, *Phylica confusa*, *Lampranthus sociorum*, *Agathosma ovata* and *Eriocephalus africanus*, as well as the shrub *Colpoön compressum*. Shrubs are wind-cropped to a maximum of 1 m, and the total aerial cover of the vegetation averages 60%. A facies, dominated by *Sporobolus virginicus* (Table 2, rel. 62), was distinguished within this community.

D. *Gazania rigens*–*Limonium scabrum* Rocky Headland Community

Salt-tolerant asteraceous *Gazania rigens* var. *uniflora* and a taxon from the *Limonium scabrum* complex accompanied by mesembs such as *Drosanthemum marinum* and *Ruschia tenella*, as well as other leaf succulents such as *Crassula* sp. and *Sarcocaulon natalense*, form an assemblage typical of the exposed rocky headlands in the southern Cape.

Community C and the rocky headland ‘herbland’ Community D have many species in common, which can be ascribed to a so-called neighbourhood effect (or mass effect; Shmida & Wilson 1985). Naturally, the exposed Community D is virtually lacking (except of *Sarcocaulon natalense*) in its ‘own’ diagnostic species because of the environmental stress in the form of deposition of

wind-borne salt that poses a major selective pressure on the potential species pool.

Due to the low altitude this community is greatly exposed to the influence of the wind and especially to salt spray (Figure 3). The vegetation has a very low cover and is wind-cropped. The average height of the vegetation is between 0.13 and 0.33 m. Of all the community types, this one is lowest in species richness with a mean of 10 species on average. Shallow soil covering granite rocks is characteristic, and is often less than 5 cm deep and very stony. Surface boulders are often present and modify the microhabitat to some degree. A facies with *Gazania rigens* var. *uniflora* was distinguished within this community (Table 2, rel. 68).

This species composition corresponds with the description of similar rocky headland communities described for other parts of the coastline at Plettenberg Bay (Hellström 1990) and Port Alfred (Lubke 1983).

Gradient analysis

The ordination of the fynbos communities (Figure 4) revealed a horseshoe structure allowing the direct recognition of a coenocline spanning two fynbos communities

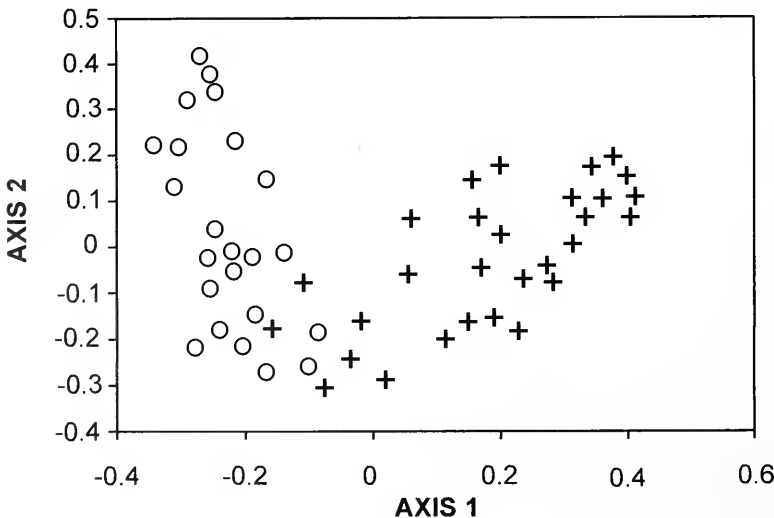


FIGURE 4.—Ordination of fynbos vegetation using Principal Coordinates Analysis. +, relevés of the *Relhania calycina*–*Phylica confusa* Fynbos Community; ○, relevés of the *Leucadendron salignum*–*Syncarpha paniculata* Fynbos Community.

TABLE 3.—Soil properties for communities (mean with standard deviation in brackets)

Soil parameter	Community			
	A	B	C	D
Moisture (%)	2.6 (2.3)	3.2 (2.8)	4.2	1.9 (1.5)
Water-holding capacity (ml/g)	0.7 (0.1)	0.9 (0.2)	0.7	0.5 (0.1)
Organic material (%)	7.0 (3.1)	12.3 (5.0)	7.8	4.4 (1.1)
pH	6.1 (0.2)	5.9 (0.2)	6.3	6.4 (0.1)
Conductivity (mS/m)	18.3 (9.2)	29.5 (18.9)	40.2	26.8 (10.5)
Coarse sand (%)	53.6 (10.9)	64.2 (6.5)	56.9	59.5 (15.9)
Medium sand (%)	11.2 (3.7)	11.0 (2.2)	14.5	13.9 (6.4)
Fine sand (%)	21.4 (6.8)	13.8 (3.2)	16.0	14.2 (6.4)
Silt (%)	11.9 (1.6)	10.1 (2.7)	6.6	8.2 (1.1)
Clay (%)	1.8 (0.8)	0.9 (0.5)	6.0	4.3 (2.0)
Number of samples	5	12	1	2

A, *Leucadendron salignum*–*Syncarpha paniculata* Fynbos Community; B, *Relhania calycina*–*Phylica confusa* Fynbos Community; C, *Pterocelastrus tricuspidatus*–*Ruschia tenella* Coastal Scrub Community; D, *Gazania rigens*–*Limonium scabrum* Rocky Headland Community.

along Axis 1 of the scatter diagram. There was a clear separation along this coenocline between the *Relhania calycina*–*Phylica confusa* Fynbos Community and the *Leucadendron salignum*–*Tetradlea cuspidata* Fynbos Community. This pattern is interpreted in terms of exposure to wind and salt spray as reflected in topographical features and soil properties.

A classification scheme accompanied by associated environmental relationships (Figure 2) suggests that the *Leucadendron salignum*–*Tetradlea cuspidata* Fynbos Community occurs on deep soils inland of the cliff summits where the vegetation is protected from wind and salt spray. The *Relhania calycina*–*Passerina vulgaris* Fynbos Community occurs on shallow, stony soils on the cliff summits, where there is a higher exposure to wind and salt spray.

Physical soil properties varied from community to community (Table 3). Cliff summits had the highest proportion of coarse sand, slopes above the cliff summits had the highest proportion of silt, and steep tallus slopes and rocky headland slopes had the highest proportions of medium sand, fine sand and clay. This is a trend in decreasing sand particle size away from the cliff summit (below and above) and larger proportion of clay to silt below the cliff summits (steep tallus slopes and rocky headland slopes).

Soil conductivity levels showed a decreasing trend as exposure to wind from the sea decreased. High levels were recorded on the steep tallus slopes, the cliff summits and the rocky headland slopes. The two cliff summit communities showed a difference in conductivity levels with the *Erioccephalus africanus* Subcommunity having higher conductivity measures than the *Tetradlea cuspidata* Subcommunity. These higher conductivity levels were attributed to higher salinity levels from wind-borne salt spray effects.

Fire appeared to play an important role in the nature of the communities especially in the *Leucadendron salignum*–*Syncarpha paniculata* Fynbos Community where the subcommunities Aa and Ab could be separated from the subcommunities Ac and Ad based on evidence of recent burning. We suggest that the subcommunities are distributed along a fire-induced succession gradient, but with site-specific effects also coming into play.

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Checklist of plant species of the coastal fynbos and rocky headlands, south of George, South Africa

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Keywords: checklist, coastal fynbos, endemics, phytogeography, rocky headlands, South Africa, Western Cape

ABSTRACT

A checklist of vascular plants and cryptograms was compiled for the fynbos and rocky headland communities of the coastal region south of George. The area studied is a 12 km stretch of steep sandstone cliffs forming alternating bays and headlands situated between Glentana and Wilderness. The plant communities of the natural vegetation inhabiting the coastline are a mixture of coastal thicket, riparian thicket, fynbos and rocky headland types. The extent of natural vegetation has been reduced by the spread of agricultural land and urban development and is under further threat from the spread of naturalised alien invader species, particularly *Acacia cyclops*. The checklist records the occurrence of 271 taxa including 16 alien species (6% of taxa). Of the flowering plant species recorded, 6% were regional or local endemics.

INTRODUCTION

The study area is a 12 km section of coastline south of George extending from Rooiklip, southeast of Pacaltsdorp, to Ghwanobaai, 3 km east of Glentana (see Hoare *et al.* 2000 for details). It includes a band of vegetation within 500 m of the high tide mark on steep sandstone cliffs which form alternating bays and headlands. The plant communities of the natural vegetation along the coastline are a mixture of coastal thicket, riparian thicket, fynbos and rocky headland types. The study was confined to the fynbos and rocky headland vegetation. Riparian thicket, dune thicket, dense alien stands and agricultural lands were not sampled. Rainfall along this section of coastline occurs throughout the year, but with three distinct peaks in spring, summer and autumn (Hoare *et al.* 2000). Because of its close proximity to the sea, vegetation structure and composition are greatly influenced by oceanic winds. The extent of the natural vegetation has been reduced by the spread of agricultural land and urban activities and is under further threat from the spread of naturalised alien species, particularly *Acacia cyclops*.

This study area falls into that part of the Fynbos Biome called Limestone Fynbos of the Mossel Bay District (Low & Rebelo 1996) of which $\pm 14\%$ is conserved and 40% transformed, although the recent proclamation of the Agulhas National Park may affect these statistics. The particular study area is of interest because of its scenic beauty and its location in the centre of the Garden Route—a popular tourist attraction. Most of the study area is owned by private landowners who have used the land mostly for agriculture (in places agricultural lands extend to within a few metres of the summit of the coastal cliffs), but also for plantation forestry on a

small scale. Urban development occurs in nodes, e.g. Herold's Bay and Victoria Bay. Recreational activities, e.g. fishing, occur on a small scale along the coast. Disturbances related to all these activities have resulted in invasion by alien trees and shrubs, particularly *Acacia cyclops*. *Pinus* species have spread from the plantations and are also a potentially serious threat.

The aim of this work was to provide a checklist of the plant species along this stretch of coastline that can act as a basic reference for floristic and ecological work and as a baseline for future development in the region. This checklist forms a link between checklists and floristic studies done for the Western Cape coastal region (Boucher 1977; Taylor 1985), southern Cape coast (Hellström 1990; Hoare 1994; Van der Merwe 1979) and the Eastern Cape coast (Lubke 1983; Lubke *et al.* 1988; Cloete & Lubke 1999). This provides the opportunity for comprehensive examination of floristic gradients along the coastal region of the Fynbos Biome.

METHODS

Fieldwork was done in all four seasons of the year to cover as many flowering times as possible. Voucher specimens of most taxa were deposited in the National Herbarium, Pretoria, and additional taxa listed were obtained from sight records made during the course of fieldwork. The herbarium collection at PRE was consulted to obtain records of plant species previously collected in the study area, and these were added to the checklist.

RESULTS

The checklist lists 271 taxa comprising nine lichen species, three bryophytes, three pteridophytes, two gymnosperms, 56 monocotyledons and 198 dicotyledons (Table 1). The most commonly represented angiosperm families (Table 2) are Asteraceae (15% of species), Poaceae (7%), Cyperaceae (6%), Fabaceae (6%), Mesembryanthemaceae (5%), Ericaceae (5%) and Crassulaceae (4%). The genera with the most species are *Erica* (11), *Crassula* (11), *Aspalathus* (8) and *Helichrysum* (6). *Ficinia*, *Lam-*

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TABLE 1.—Number of families, genera and species recorded in the vegetation of the coast south of George

	Families	Genera	Indigenous spp.	Naturalised alien spp.
Lichens		4	9	0
Bryophytes	3	3	3	0
Pteridophytes	3	3	3	0
Gymnosperms	1	1	0	2
Angiosperms				
Dicotyledons	52	107	187	11
Monocotyledons	10	41	53	3
Total	69	159	255	16

pranthus, *Phylica* and *Hermannia* were each represented by five species.

All of the 20 largest genera listed for the Cape flora by Bond & Goldblatt (1984) are represented in this coastal area, as are 13 of the 15 largest families. Of the 16 alien species recorded, *Acacia cyclops* was by far the most abundant.

Some 230 flowering plant species were classified according to phytogeographical range and affinity (Table 3). It was found that 35% are endemic to the Fynbos Biome and 7% are regional (southern Cape) endemics and one was a local endemic—*Silene vlokii*, which has a restricted range from Herold’s Bay to Glentana.

DISCUSSION

Asteraceous Coastal Fynbos is defined as having high asteraceous and non-ericaceous ericoid cover and often high grass cover (Cowling 1992). *Phylica*, *Passerina*, *Agathosma* (and other Diosminae), *Aspalathus*, *Restio* and *Cliffortia* are listed as dominant genera in this vegetation type (Cowling 1992), a view which is consistent with what was found in the study area (Hoare *et al.* 2000).

A comparison of the flora of the study area with those of the Goukamma Nature Reserve (Table 4) shows that the number of species and genera in the present study area is comparatively high in relation to its size, especially considering that not all vegetation types were sampled. Goukamma Nature Reserve is a larger area but with

TABLE 2.—Families of angiosperms in the study with the highest number of genera and species

Family	No. genera	No. spp.
Asteraceae	25	39
Poaceae	12	17
Cyperaceae	8	16
Fabaceae	7	16
Mesembryanthemaceae	7	14
Ericaceae	3	13
Crassulaceae	2	11
Iridaceae	8	9
Santalaceae	3	7
Thymelaeaceae	2	5
Sterculiaceae	1	5

TABLE 3.—Distribution of angiosperms found in the study area

Distribution	No. spp.
Endemic to Fynbos Biome	81
Regional endemics (southern Cape)	15
Local endemics	1

TABLE 4.—Comparison of the indigenous angiosperm flora of the study area with nearby Goukamma Nature Reserve (Van der Merwe 1979; Hoare 1994)

	Study area	Goukamma Nature Reserve
Area (km ²)	1.9	14.6
No. genera	136	121
No. spp.	254	168
No. spp. per genus	1.7	1.4
No. spp. per km ²	134	11.5

fewer species, indicating that there is lower diversity in the Dune Fynbos and thicket vegetation of that region compared with the communities along the rocky shore and promontories of this study area. This coastal region therefore has a surprisingly high diversity for such a small area, probably due to its abundance of microhabitats. Further studies encompassing the non-fynbos vegetation types should be carried out to contribute to the knowledge of this relatively understudied and poorly conserved region.

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CHECKLIST

Taxa are arranged alphabetically, and author citations follow Brummitt & Powell (1992). Except for site records, collectors' names and numbers follow the author citation; specimens are housed at PRE. Naturalised alien species are marked with an asterisk*. Abbreviations for collectors' names: *Bo*, P. Bohnen; *Da*, G. Davidse; *Th*, M.F. Thompson; *V*, J.E. Victor; *VFC*, C.M. Van Wyk, A. Fellingham & M. O'Callaghan; *V&H*, J.E. Victor & D.B. Hoare; *Wi*, I.J.M. Williams.

LICHENS

Cladia aggregata (Sw.) Nyl., V 327
Cladonia
 Chasmariae sp., V 328
 chlorphaea (Floerke) Spreng., V 325
 Cocciferae sp., V 326
 confusa R.Sant., V 324
 coniocraea (Floerke) Spreng., V 328b
Pycnoporus sp., V 545
Teloschistes flavicans (Sw.) Norm., V 546
Usnea rubicunda Stirt., V 547

BRYOPHYTES

FUNARIACEAE
Funaria hygrometrica Hedw., V 290
PHYLOGONIACEAE
Catagonium nitens (Brid.) Card. subsp. *maritimum* (Hook.) S-H Lin, V 352
POTTIACEAE
Tortella xanthocarpa (C.Muell.) Broth., V 303

PTERIDOPHYTES

ADIANTACEAE
Cheilanthes hirta Sw. var. *hirta*, V 367
ASPLENIACEAE
Asplenium rutifolium (P.J.Bergius) Kunze, V 351, 366
SCHIZAEACEAE
Schizaea pectinata (L.) Sw., V 317

GYMNOSPERMS

PINACEAE
Pinus
 **pinaster* Aiton
 **radiata* D.Don

ANGIOSPERMS: MONOCOTYLEDONS

ASPHODELACEAE
Anthericum cooperi Baker, V 561; V&H 43
CYPERACEAE
Ficinia
 albicans Nees, V&H 83
 cf. *gracilis* (Poir.) Schrad., V 259, 321, 329, 359
 lacinata (Thunb.) Nees, Da 33719
 nigrescens (Schrad.) J.Raynal, V 261, 285; V&H 68
 repens (Nees) Kunth, V 292
Fuirena hirsuta (P.J.Bergius) P.L.Forbes, V 306
Isolepis tenuissima (Nees) Kunth, V 288
Mariscus
 congestus (Vahl) C.B.Clarke, V 557
 thunbergii (Vahl) Schrad., V 282
Pycnus polystachyos (Rottb.) Beauv. var. *polystachyos*, V 287
Schoenoxiphium sparteum (Wahlenb.) C.B. Clarke, Da 33726
Tetragia
 bolusii C.B.Clarke, VFC 234
 compressa Turrill, V 246; V&H 40
 cuspidata (Rottb.) C.B.Clarke, V 242; V&H 78
 microstachys (Vahl) Pfeiffer, V 309, 316, 333
Trianoptiles capensis (Steud.) Harv., V 289
HYACINTHACEAE
Lachenalia bulbifera (Cyr.) Engl., VFC 170
Ornithogalum sp.
HYPOXIDACEAE
Empodium sp., V 207
Spiloxene trifurcillata (Nel) Fourc., V 335

IRIDACEAE
Babiana fourcadei G.J.Lewis, V 349
Bobartia aphylla (L.f.) Ker Gawl., V 307, 540; V&H 47
Chasmanthe aethiopica (L.) N.E.Br., VFC 171
Freesia
 alba (G.L.Mey.) Gumbleton
 leichtlinii Klatt, V 296
Gladiolus floribundus Jacq. subsp. *floribundus*, Th 609
Hesperantha falcata (L.f.) Ker Gawl., V 213
Micranthus alopecuroides (L.) Rothm., V 558
Tritoniopsis antholyza (Poir.) Goldblatt, V 495

JUNCACEAE
Juncus
 acutus L. subsp. *leopoldii* (Parl.) Snog., V 345
 dregeanus Kunth, V 286, 534

ORCHIDACEAE
Disperis capensis (L.) Sw. var. *capensis*, V 238
Herschelianthe hians (L.f.) Rauschert, V 529, 533

POACEAE
Cynodon dactylon (L.) Pers., V 516
Eragrostis
 capensis (Thunb.) Trin., V 503
 plana Nees, V 511
Ehrharta
 calycina J.E.Sm., V 513
 capensis Thunb., V 513b; V&H 80
 erecta Lam. var. *erecta*
 *Lolium *perenne* L., V 524
Paspalum
 *dilatatum Poir., V 522
 distichum L., V 517
Pentastchitis eriostoma (Nees) Stapf
Polypogon strictus Nees, V 350
Setaria sphacelata (Schum.) Moss var. *sphacelata*, V 523
Sporobolus
 africanus (Poir.) Robyns & Tournay, V 518
 virginicus (L.) Kunth
Stenotaphrum secundatum (Walt.) Kuntze
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 spicata L.f. var. *spicata*, V 338
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Athanasia trifurcata (L.) L., V 509
Athrixia capensis Ker Gawl., V 541
Berkheya armata (Vahl) Druce, V 531
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Pterocelastrus tricuspidatus (Lam.) Sond., V 299
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- southii* Schönland subsp. *sphaerocephala* Tölken, V 223
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- crispa* (Thunb.) Guericke subsp. *crispa*, V 368
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laxa Sond., VFC 218
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- alopecurus* Benth., V 353; V&H 56
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asparagoides L.f. subsp. *rubro-fusca* (Eckl. & Zeyh.) R.Dahlgren, V 331
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GENTIANACEAE

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Monopsis unidentata (Dryand.) E.Wimm. subsp. *unidentata*, V 515

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- brevifolium (*Aiton*) *Schwantes*, V 222
- sp., V&H 63

Lampranthus

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- sp., V 220

Conophytum bilobum (*Marloth*) *N.E.Br.*, VFC 176

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Myrica quercifolia *L.*

MYRTACEAE

*Leptospermum laevigatum (*Caertn.*) *F.Muell.*, V 264

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Oxalis spp., V 310, 224

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Limonium scabrum (*Thunb.*) *Kuntze* var. scabrum, V&H 60

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Muraltia ericoides (*Burm.f.*) *Steud.*, V 499

Polygala

- fruticosa *P.J.Bergius*, V 295
- microlopha *DC.* var. gracilis *Levyns*, V 314
- myrtifolia *L.*, V 346

PRIMULACEAE

*Anagallis arvensis *L.*, V 291, 519

PROTEACEAE

*Hakea sericea *Schrad.*, V 361

Protea neriifolia *R.Br.*, V 237

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Knowltonia vesicatoria (*L.f.*) *Sims* subsp. grossa *H.Rasm.*, V 340

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- var. maritima *Pillans*, VFC 228
- confusa *Pillans*, V&H 50
- purpurea *Sond.* var. pearsonii *Pillans*, V 245
- strigulosa *Sond.*, V&H 29

ROSACEAE

Cliffortia

- falcata *L.f.*, V 265
- serpyllifolia *Cham. & Schlechtd.*, V 228, 542
- sp., V 313

RUBIACEAE

Anthospermum

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- prostratum *Sond.*, V 251

RUTACEAE

Agathosma

- apiculata *G.F.W.Mey.*, V 275
- capensis (*L.*) *Dümmer*, V 312
- ovata (*Thunb.*) *Pillans*, V 232, 337

Euchactis burchellii *Dümmer*, Wi 2310

SANTALACEAE

Colpoon compressum *P.J.Bergius*, V 229, 342

Thesidium

- fragile (*Thunb.*) *Sond.*
- microcarpum (*A.DC.*) *A.DC.*, V 231, 298
- podocarpum (*A.DC.*) *A.DC.*, V 278

Thesium

- lisae-mariae *Stauffer*, V 330
- nigromontanum *Sond.*, V&H 51
- sertulariastrum *A.W.Hill*, V 226
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Phyllopodium rustii (*Rolfe*) *Hilliard*, V 284

Sutera

- hispida (*Thunb.*) *Druce*, VFC 163a
- sp., V 277, 339

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Selago

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- dregei *Rolfe*, VFC 209
- sp. nov., V 234, 496

SOLANACEAE

Solanum rigescens *Jacq.*, VFC 178

STERCULIACEAE

Hermannia

- althaeifolia *L.*, V 250
- angularis *Jacq.*, V 256, 535
- holosericea *Jacq.*, V 539
- lavandulifolia *L.*, V 283
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THYMELAEACEAE

Passerina

- falcifolia *C.H.Wright*, V 556
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Struthiola

- ciliata (*L.*) *Lam.* subsp. angustifolia (*Lam.*) *Peterson*, V 216
- parviflora *Meisn.*, V 497
- striata *Lam.*, V 504; V&H 73

TILIACEAE

Grewia occidentalis *L.*, V 521

VERBENACEAE

*Verbena bonariensis *L.*, V 506

VISCACEAE

Viscum capense *L.f.* subsp. hoolei *Wiens*, V 225

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Zygophyllum morgsana *L.*, V 274, 369

Miscellaneous notes

POACEAE

APOMICTIC EMBRYO SAC DEVELOPMENT IN *CENCHRUS CILIARIS* (PANICOIDEAE)

Apomixis is distributed throughout the plant kingdom and is known in over 300 species of at least 35 different families (Hanna & Bashaw 1987). Research on apomixis is in grasses began in the early 1930's with *Poa pratensis* L. (Müntzing 1933). Apomixis is especially prevalent among perennial forage grasses and has been reported in more than 125 species representing most of the tribes. Well-known apomictic grasses include *Paspalum dilatatum* Poir. (Snyder 1957), *P. notatum* Fluegge (Snyder 1957), *Setaria* P.Beauv. (Emery 1957) and *Cenchrus ciliaris* L. (Fisher *et al.* 1954; Snyder *et al.* 1955). Apomixis in the angiosperms means asexual reproduction by seeds (Nogler 1984). In this study reduced embryo sacs (embryo sacs in which meiosis occurs) imply sexual reproduction, whereas unreduced embryo sacs imply asexual or apomictic reproduction.

The aim of this study is to determine whether reduced embryo sacs are formed in *C. ciliaris* specimens included in this study. The type of embryo sac will give an indication of the sexual or apomictic nature of the species and will suggest to what extent cross-fertilisation contributed to the genetic variation in this species.

MATERIAL AND METHODS

The plant material used in this study was collected in the field (Table 1). A selection from the material, collected for meiotic analysis, was used to study embryo sac development. Florets in various developmental stages were used. Inflorescences were dehydrated with ethanol and tertiary butanol before being embedded in pastulated Paraffin wax. Sections (6 µm) were cut with a rotary microtome, mounted and stained with a modified (Spies & du Plessis 1986) safranin (Johansen 1940) and fast green (Sass 1951) procedure. A minimum of twenty embryo sacs per developmental stage were studied in each specimen. A Nikon photomicroscope and Ilford Pan-F film (ASA 50) were used for the photomicrographs.

RESULTS

Embryo sac development was studied in 27 specimens, representing four different ploidy levels (Table 1) The nucellus was multiseriate and protected by various

TABLE 1.—List of *Cenchrus ciliaris* specimens with *Panicum* type of embryo sacs, their localities and their chromosome number (B-chromosomes are abbreviated as B)

2n =	Locality	Voucher
34	2627 (Potchefstroom): in Potchefstroom, on route to Orkney, (–CA)	Spies 5883
36	2624 (Vryburg): near Vryburg, on route to Kuruman, (–DC) 2723 (Kuruman): 16 km from Kuruman to Vryburg, (–BC) 2724 (Taung): 101 km from Kuruman to Vryburg, (–AB) 2725 (Bloemhof): 2 km from Britten to Christiana, (–CB) 2822 (Glen Lyon): 7 km from Smidsdrift to Postmasburg, (–DA) 2822 (Glen Lyon): 25 km from Bloemfontein to Brandfort, (–CD) 2925 (Jagersfontein): 56 km from Petrusburg to Kimberley, (–AA) 3222 (Beaufort West): 5 km from Beaufort West, (–BC) 3224 (Graaff-Reinet): 58 km from Jansenville to Graaff-Reinet, (–BC) 3224 (Graaff-Reinet): 131 km from Uitenhage to Graaff-Reinet, (–DC) 3224 (Graaff-Reinet): 145 km from Uitenhage to Graaff-Reinet, (–DC) 3324 (Steytlerville): 102 km from Uitenhage to Graaff-Reinet, (–BD)	Spies 5529 Spies 5525 Spies 5527 Spies 5542, 5543 Spies 5521 Spies 5577 Spies 5509 Spies 5487 Spies 5240 Spies 5236 Spies 5237 Spies 5232
36+0–2B	2624 (Vryburg): near Vryburg, on route to Kuruman, (–DC) 2925 (Jagersfontein): 60 km from Petrusburg to Kimberley, (–AA) 3125 (Steynsburg): 10 km from Steynsburg to Hofmeyer, (–BC) 3222 (Beaufort West): 5 km from Beaufort West, (–BC) 3324 (Steytlerville): 68 km from Uitenhage to Graaff-Reinet, (–DA) 3325 (Port Elizabeth): 30 km from Uitenhage to Graaff-Reinet, (–CD)	Spies 5531 Spies 5512 Spies 5584 Spies 5488 Spies 5231 Spies 5229
45	2522 (Sanie): in the riverbed at Watersend, (–DB) 3024 (Colesberg): 27 km from Verwoerd Dam to Venterstad, (–DA) 3224 (Graaff-Reinet): 39 km from Jansenville to Graaff-Reinet, (–DA) 3224 (Graaff-Reinet): 15 km from Jansenville to Graaff-Reinet, (–DC)	Spies 5497 Spies 5581, 5583 Spies 5239 Spies 5238
54	2824 (Kimberley): 1 km from Kimberley to Griekwastad, (–DA)	Spies 5514
54+0–1B	2824 (Kimberley): 1 km from Kimberley to Griekwastad, (–DA)	Spies 5517

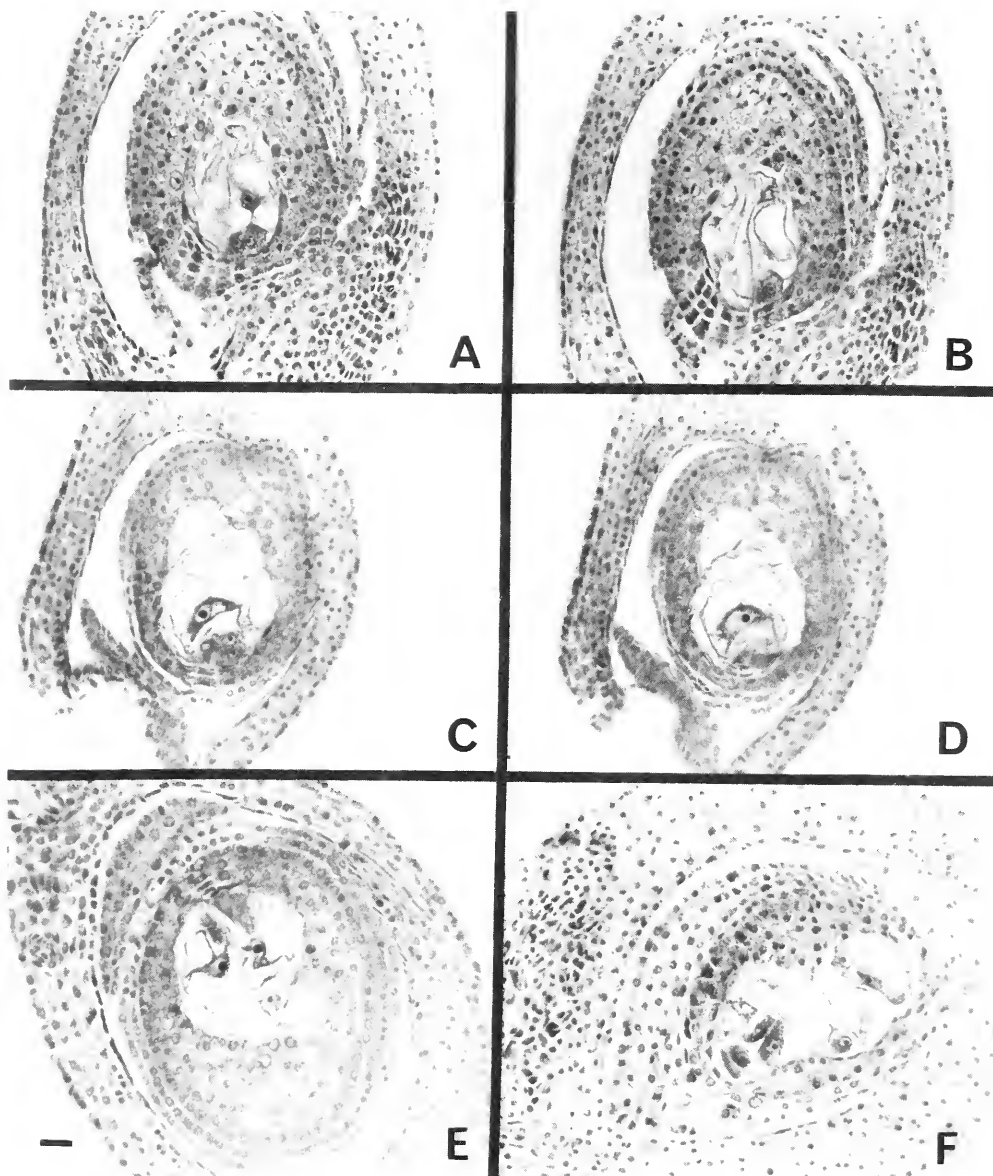


FIGURE 1.—Photomicrographs of un-reduced embryo sac development of the *Panicum* type in ovules of *Cenchrus ciliaris*. A, B, *Spies 5240*: A, three embryo sacs in ovule with only two visible in this section, two nuclei in micropylar region of one embryo sac resembling either an egg nucleus and a synergid or two synergids, with one chalazal polar nucleus; B, next section of ovule in A, three embryo sacs visible; third nucleus of embryo sac in A in micropylar region, representing either an egg or a synergid. C–E, *Spies 5232*: C, two embryo sacs per ovule; two nuclei in micropylar region, resembling an egg nucleus and a single synergid, with one chalazal polar nucleus; D, second section of ovule in C with a second polar nucleus in chalazal region of embryo sac; E, at least four un-reduced embryo sacs in mature ovule. F, *Spies 5488*, at least five un-reduced embryo sacs in mature ovule. Scale bar: 10µm.

multicellular integuments. Some of the integuments completed their development at a relatively late stage. The archesporial cell functioned directly as the primary megasporocyte. One or more somatic cells with prominent nuclei, lying in the centre of the nucellus, also enlarged. These cells soon obscured all traces of the degenerated gametophyte. These cells had dense cytoplasm and were usually adjacent to the sporogenous material. The nuclei of the aposporous cells underwent one to several divisions and formed a well-defined dyad.

The aposporic embryo sacs are extremely vacuolated and mature embryo sacs usually contained four nuclei. Some of the nuclei resembled the egg and polar cells of a reduced embryo sac. These embryo sacs usually included one polar nucleus, an egg nucleus and two synergid cells (Figure 1A, B). Some embryo sacs included an egg nucleus, one synergid cell and two polar nuclei (Figure 1C, D). These un-reduced embryo sacs were classified as four nucleated *Panicum* type aposporic embryo sacs (Figure 1A, D).

The total number of aposporic embryo sacs per ovule varied among the specimens studied (Figure 1E, F). A maximum of eight aposporic embryo sacs per ovule was observed (*Spies 5239*). These multiple embryo sacs were usually concentrated in the central part of the ovule and, at maturity, occupied most of the former region of the nucellus (Figure 1E, F).

DISCUSSION

The mechanism of apospory in *C. ciliaris* involves the development of the embryo from an unreduced nucleus, in an embryo sac derived from a somatic cell in the ovary. These aposporous embryo sacs may develop in the nucellus of the ovule or in some species in the integuments and ovary wall (Bashaw & Hanna 1990). Apospory is the apomictic mechanism most common in the grasses, particularly in the tribe Paniceae, which accounts for more than 95% of known apomictic species (Bashaw & Hanna 1990). The origin of aposporous cells in the grass ovule is quite different from the normal pattern of sexual megasporogenesis (Bashaw 1980). Early development of the megaspore mother cell is usually identical in aposporous and sexual ovules. In both cases, the megaspore mother cell differentiates in the hypodermal layer of the nucellus in the micropylar region, during the enlargement stage of the young ovule. Meiosis in both aposporous and sexual ovules generally results in a linear tetrad. The similarity between apospory and sexual embryo sac development ends at this point (Bashaw & Hanna 1990).

Aposporic development in *C. ciliaris* is initiated by the unusual enlargement of one or more somatic (nucellar) cells. These cells, in comparison to the normal nucellar cells, usually have prominent nuclei and dense cytoplasm. The nucleus of the aposporous cell initially undergoes one to several mitotic divisions. The degree of differentiation of aposporous embryo sacs in *C. ciliaris* varies. In some grass species, one or more of the aposporous sacs may develop to the extent that they closely resemble the typical sexual embryo sac (Bashaw & Hanna 1990). This is not the case in *C. ciliaris*, for a four-nucleated embryo sac was most often observed (Figure 1A–D). This included a polar nucleus, an egg nucleus and two synergid cells (Figure 1A, B) or one egg, one synergid and two polar nuclei (Figure 1C, D). Antipodal cells were completely lacking. The embryo sacs observed were, therefore, classified as unreduced aposporic embryo sacs, of the *Panicum* type. This finding corresponds with previous reports by various authors (Bashaw & Holt 1958; Brown & Emery 1958; Bashaw 1962) and is typical of the Panicoideae (Bashaw & Hanna 1990; Mogie 1992). The number of embryo sacs of nucellar origin varied from two to eight in *Spies 5239*. Occasionally observed, was a cluster of unreduced embryo sacs which could not be accurately counted.

Various authors have reported a number of ovules in *C. ciliaris* containing a single aposporous embryo sac in the nucellus (Fisher *et al.* 1954; Bashaw & Hanna 1990). According to their reports, these sacs were centrally located, in the micropylar region of the ovule, and occupied more or less the same location and total area as the

sexual gametophyte in sexual plants of this species. This type of embryo sac development was not observed in the current study, in which the minimum number of embryo sacs present in the ovule, was two.

The variation in the arrangement of structures of the aposporous embryo sacs (Figure 1A–D) is characteristic of *C. ciliaris*. This embryological variation corresponds with the variation observed on chromosome level (Visser *et al.* 1998a, b, c). This species is morphologically (De Lisle 1963) and cytogenetically highly polymorphic and complex. Chromosome abnormalities, observed during meiosis, and varying polyploid levels were common (Visser *et al.* 1998a, b, c). The various polyploid natures (varying from autosegmental-allopolyploidy to pure allopolyploidy) indicated the presence of hybridization (Visser *et al.* 1998a, b, c). However, during this study, no correlation was found between ploidy level and embryo sac development or cell morphology during embryo sac development. The absence of any suggestion of sexual reproduction in the specimens studied, indicates either that the genetic variation originated before these plants became obligate apomicts, or that the frequency of sexuality is extremely low. The latter possibility is contradicted by the genetic variation observed in these specimens.

When Taliaferro & Bashaw (1966) discovered a sexual plant, they investigated the inheritance of apomixis in *C. ciliaris*. The plant was an obligate sexually reproducing specimen, but heterozygous for the method of reproduction. The progeny, after selfing, was either obligate sexual or obligate apomictic, indicating the heterozygous nature of this specimen. Based on their data, Bashaw & Hanna (1990) suggested that the mode of reproduction is controlled by two different genes, with epistasis favouring dominant expression of the gene for sexuality. They proposed that the genotype of the sexual plant was AaBb and that of the two apomictic cultivars were Aabb. Their hypothesis assumed that dominant gene B conditions sexual reproduction and is epistatic to dominant gene A, which conditions apospory. Due to the absence of dominant gene A, a double recessive aabb was expected to reproduce sexually. Gene A, therefore, controls all of the processes resulting in development of unreduced nucellar embryo sacs and abortion of the normal sexual sporogenous tissue (Bashaw & Hanna 1990).

The genetic inheritance of apomixis suggests that a small percentage of sexual plants representing *C. ciliaris* may still prevail in nature. It is accepted that sexual or partially sexual plants probably exist in most apomictic species. Based on this fact, facultative apomicts are claimed to precede obligate apomicts in the development of the agamic complex (Bashaw & Hanna 1990). Clausen (1954) described facultative apomixis as an evolutionary equilibrium system in which the apomictic process is in balance with an almost dormant sexual process, which can be invoked and can release a part of the stored sexual variability for a certain period. In the geographic distribution of *C. ciliaris*, completely sexual, facultative and obligate plants may still be present. Sexually reproducing plants serve as foundation for the considerable genetic variation found among, and in, populations representing this species. Facultative apomictic

plants are, therefore, a seemingly dormant but effective source of variation, for heterozygous genotypes are produced each time when sexual and apomictic plants hybridize (Bashaw *et al.* 1970).

Although no reduced embryo sacs (suggesting sexual reproduction) were observed during the current study, chromosomal and morphological differences were observed in plants representing a specific region. This indicates that a small percentage of specimens of *C. ciliaris* have to be facultative apomicts, for the offspring were not exact replicas of the maternal plants. It is concluded that both facultative and obligate apomixis are present in *C. ciliaris*. This conclusion is based on the presence of more genetic variation than can be accounted for by mutations alone. There may also be sexual specimens in nature, but they were not found and sampled during this study.

CONCLUSIONS

Apospory as a mode of asexual reproduction is common in the Poaceae. It involves the development of an embryo from an unreduced nucleus, in an embryo sac derived from a somatic cell. Aposporic development in *C. ciliaris* varies, for this type of development is initiated in various somatic cells simultaneously, and leads to the maturing of various numbers of embryo sacs in the ovule.

Embryological variations regarding embryo sac development were observed in this species. These aposporous embryo sacs were characterized as unreduced four-nucleated embryo sacs of the *Panicum* type. Although the presence of cytogenetic and morphological variation indicates that this species may be characterized as a facultative apomictic species, all ploidy levels appear to be obligate apomicts. This suggests that the morphological and/or genetic variation originated before obligate apomixis occurred.

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HYACINTHACEAE

CHROMOSOME STUDIES ON AFRICAN PLANTS. 13. *LACHENALIA MUTABILIS*, *L. PUSTULATA* AND *L. UNICOLOR*

The genus *Lachenalia* Jacq.f. ex Murray consists of small bulbous geophytes and shows a great potential for use as pot plants (Niederwieser *et al.* 1997). Various chromosome numbers, and even different basic chromosome numbers, have been reported for this genus (Moffett 1936; De Wet 1957; Riley 1962; Mogford 1978; Ornduff & Watters 1978; Nordenstam 1982; Crosby

1986; Hancke & Liebenberg 1990; Hancke 1991; Johnson & Brandham 1997; Kleynhans 1997; Hancke & Liebenberg 1998; Kleynhans & Spies 1999).

Lachenalia mutabilis Sweet belongs to the *L. orchoides* group (Crosby 1986) and the chromosome numbers reported for this species vary from $2n = 10$

(Ornduff & Watters 1978; Johnson & Brandham 1997) to $2n = 14$ (De Wet 1957; Johnson & Brandham 1997) and 56 (De Wet 1957).

Lachenalia pustulata Jacq. and *L. unicolor* Jacq. are closely related species, growing in the southwestern Cape. Both species are classified as part of the *L. unicolor* group (Crosby 1986), and Duncan (1988) suggested that these species might be combined, due to their morphological similarities. Somatic chromosome numbers of $2n = 16$ have been reported for both species by De Wet (1957), Hancke (1991), Johnson & Brandham (1997) and Kleynhans (1997).

The aim of this paper is to determine the chromosome numbers of the three species and to determine whether any correlation exists between chromosome number and geographical distribution.

MATERIALS AND METHODS

Specimens were collected in the field throughout the geographical distribution area of each species and vegetative material of each plant collected was grown separately in the nurseries of ARC Roodeplaat and the Department of Botany and Genetics, University of the Orange Free State, Bloemfontein. Voucher specimens are housed in the Geo Potts Herbarium (BLFU) at the university (Table 2).

Bulbs were grown on Deco gel™ and actively growing root tips were cut and placed in water at 4°C for 24 hours. The root tips were fixed in Carnoy's (1886) fixative for 24–36 hours, hydrolysed in 1N HCl at 60°C for 7 minutes and stained with 0.5% leucobasic fuchsin for two hours (Darlington & LaCour 1976). Squashes were made in 1% aceto-orcin (Darlington & LaCour 1976). Slides were permanently mounted in Euparal (Darlington & LaCour 1976).

RESULTS AND DISCUSSION

Lachenalia mutabilis: this species is morphologically extremely variable. It is naturally distributed throughout Namaqualand to south of Riviersonderend (Duncan 1988). During this study 35 specimens, representing 16 populations have been studied cytogenetically. The specimens studied represent the central and northern geographical distribution area of this species (Figure 2).

Somatic chromosome numbers of 12 (Figure 3A, B), 14 (Figure 3C–G) and 24 (Figure 3H) were observed during this study (Table 2). The numbers based on $x = 7$ confirm a previous report on this species (De Wet 1957). The numbers based on $x = 6$ present a new basic chromosome number for this species. Although collected in the same geographical area as the two specimens studied by Ornduff & Watters (1978), no specimens with $x = 5$ were observed during this study. Six further specimens from unknown localities with $2n = 10$ were studied by Johnson & Brandham (1997).

Different specimens collected in a given locality showed no variation in chromosome number. Specimens

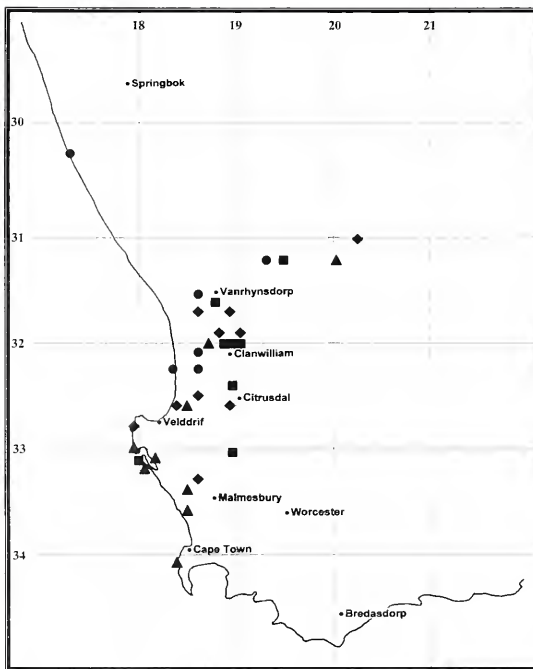


FIGURE 2.—Geographical distribution of the *Lachenalia* populations. *Lachenalia mutabilis* specimens, $x = 6$, ●; $x = 7$, ■, *L. pustulata*, ▲; *L. unicolor*, ◆.

with lower chromosome numbers were mostly collected in the northern and western areas of the geographical distribution area of this species (Figure 2). However, an insufficient number of specimens has been studied to test the validity of this observation.

Three hypotheses regarding the origin of the different basic chromosome numbers in one species can be postulated: 1, the original basic chromosome number is 5 and the misidentification of B-chromosomes is responsible for the higher basic numbers described; 2, the original basic chromosome number is 7 and dysploidy leads to the formation of lower basic chromosome numbers; or 3, an aneuploid series occurs.

The presence of B-chromosomes in various *Lachenalia* species has been reported by Hancke & Liebenberg (1990) and Johnson & Brandham (1997). Initial meiotic studies indicate that the same number of chromosomes is present in the anthers and in the root tips used during this study. The initial meiotic study also indicates normal meiosis with the formation of bivalents only. Therefore, we reject the hypothesis that misinterpretation of B-chromosomes attributed to the 'different basic chromosome numbers' observed in this species.

Johnson & Brandham (1997) suggested that the different basic chromosome numbers in *L. mutabilis* can be attributed to Robertsonian translocations resulting in dysploidy. However, the chromosome morphology of the specimens varies. Most specimens contain 4 to 8 very short chromosomes. The number of short chromosomes varies between different localities and even between specimens collected at the same locality. There is no indication of longer chromosomes (as a result of Robert-

TABLE 2.—Somatic chromosome numbers of *Lachenalia* specimens with their voucher numbers and localities. Specimens are listed according to their locality from north to south and from west to east

Voucher	2n	Locality
<i>L. mutabilis</i>		
<i>Spies 6750</i>	24	NORTHERN CAPE.—3017 (Hondeklipbaai): near Hondeklipbaai, (–AD).
<i>Spies 6744</i>	12	WESTERN CAPE.—3118 (Vanhynsdorp): near Vanhynsdorp, (–DA).
<i>Spies 6748, 6753</i>	14	WESTERN CAPE.—3118 (Vanhynsdorp): near Vanhynsdorp, (–DA).
<i>Spies 6746</i>	12	NORTHERN CAPE.—3119 (Calvinia): on top of Vanhyns Pass, (–AC).
<i>Spies 6757–6761</i>	14	NORTHERN CAPE.—3119 (Calvinia): along road to Oorlogskloof, (–AC).
<i>Spies 6774, 6775</i>	12	WESTERN CAPE.—3218 (Clanwilliam): Clanwilliam Nature Reserve, (–AB).
<i>Spies 6751</i>	12	WESTERN CAPE.—3218 (Clanwilliam): near Elandsbaai, (–AD).
<i>Spies 6747, 6767–6770, 6773, 6776–6778</i>	14	WESTERN CAPE.—3218 (Clanwilliam): near Clanwilliam, (–BB).
<i>Spies 6779–6781</i>	12	WESTERN CAPE.—3218 (Clanwilliam): near Sandberg, (–BC).
<i>Spies 6745</i>	14	WESTERN CAPE.—3219 (Wuppertal): near Citrusdal, (–CA).
<i>Spies 6784, 6785</i>	14	WESTERN CAPE.—3318 (Cape Town): Langebaan Nature Reserve, (–AA).
<i>Spies 6752</i>	14	WESTERN CAPE.—3318 (Cape Town): near Porterville, (–BB).
<i>Spies 6749, 6754–6756, 6782, 6783</i>	14	Unknown.
<i>L. pustulata</i>		
<i>Spies 6806, 6807</i>	16	NORTHERN CAPE.—3119 (Calvinia): Oorlogskloof, (–AC).
<i>Spies 6792</i>	16	WESTERN CAPE.—3218 (Clanwilliam): Algeria, (–BB).
<i>Spies 6789</i>	16	NORTHERN CAPE.—3220 (Sutherland): near Aurora, (–DC).
<i>Spies 6788</i>	16	WESTERN CAPE.—3317 (Saldanha): near Saldanha, (–BB).
<i>Spies 6808–6811</i>	16	WESTERN CAPE.—3318 (Cape Town): Langebaan, (–AA).
<i>Spies 6798–6804, 6816–6823</i>	16	WESTERN CAPE.—3318 (Cape Town): Langebaan Nature Reserve, (–AA).
<i>Spies 6790</i>	16	WESTERN CAPE.—3318 (Cape Town): near Postberg, (–AA).
<i>Spies 6791</i>	16	WESTERN CAPE.—3318 (Cape Town): near Darling, (–AD).
<i>Spies 6797</i>	16	WESTERN CAPE.—3318 (Cape Town): Mamre Road, (–BC).
<i>Spies 6787</i>	16	WESTERN CAPE.—3318 (Cape Town): near Kampsbaai, (–CD).
<i>Spies 6786, 6793, 6795, 6796, 6805, 6812–6815</i>	16	Unknown.
<i>Spies 6794</i>	16/32	Unknown.
<i>L. unicolor</i>		
<i>Spies 6827</i>	16	WESTERN CAPE.—3118 (Vanhynsdorp): Vredendal, (–CB).
<i>Spies 6828</i>	16	WESTERN CAPE.—3118 (Vanhynsdorp): Unionskraal, (–DB).
<i>Spies 6831</i>	16	NORTHERN CAPE.—3119 (Calvinia): Nieuwoudtville, (–AC).
<i>Spies 6853–6856</i>	16	WESTERN CAPE.—3217 (Vredenburg): Abdolsbaai, (–DD).
<i>Spies 6829</i>	16	WESTERN CAPE.—3218 (Clanwilliam): Verlorevlei, (–AD).
<i>Spies 6857</i>	16	WESTERN CAPE.—3218 (Clanwilliam): near Clanwilliam, (–BB).
<i>Spies 6837, 6838</i>	16	WESTERN CAPE.—3218 (Clanwilliam): Velddrif, (–CC).
<i>Spies 6825</i>	16	WESTERN CAPE.—3218 (Clanwilliam): Piketberg, (–DD).
<i>Spies 6844–6846</i>	16	NORTHERN CAPE.—3220 (Sutherland): Aurora, (–DC).
<i>Spies 6835</i>	16	WESTERN CAPE.—3318 (Cape Town): Darling, (–AD).
<i>Spies 6833, 6834, 6843</i>	16	WESTERN CAPE.—3318 (Cape Town): Porterville, (–BB).
<i>Spies 6830</i>	16	WESTERN CAPE.—3319 (Worcester): Tulbach, (–AC).
<i>Spies 6824, 6826, 6832, 6836, 6839–6842, 6847–6852</i>	16	Unknown.

sonian translocations) in any specimen or in specimens with a particular basic chromosome number. Therefore, no evidence supports the second hypothesis.

At this stage it seems as if an aneuploid series exists in *L. mutabilis*. To test this hypothesis, thorough meiotic studies, including hybrids between some of these specimens, should be completed. The use of *in situ* hybridization techniques will also help to determine the mode of chromosome evolution in this species. Simultaneously, the species delimitation should be investigated to determine whether *L. mutabilis* represents one variable species or more than one species, each with its own basic chromosome number.

Polyploidy was observed in a specimen with $x = 6$ during this study and De Wet (1957) observed it in one with $x = 7$. The tetraploid number obtained during this study was restricted to a single bulb. All other bulbs obtained from the original specimen proved to be diploid. The polyploidization process occurred consequently, during cultivation. In contrast, De Wet (1957) described an octoploid specimen, suggesting that various polyploidization processes occurred in nature. More specimens should be studied before any conclusions regarding polyploidy in this species can be made. Polyploidy is relatively scarce in this species with only two specimens (5%) exhibiting this phenomenon. Further studies are needed to determine the mode of chromosome evolution in *L. mutabilis*.

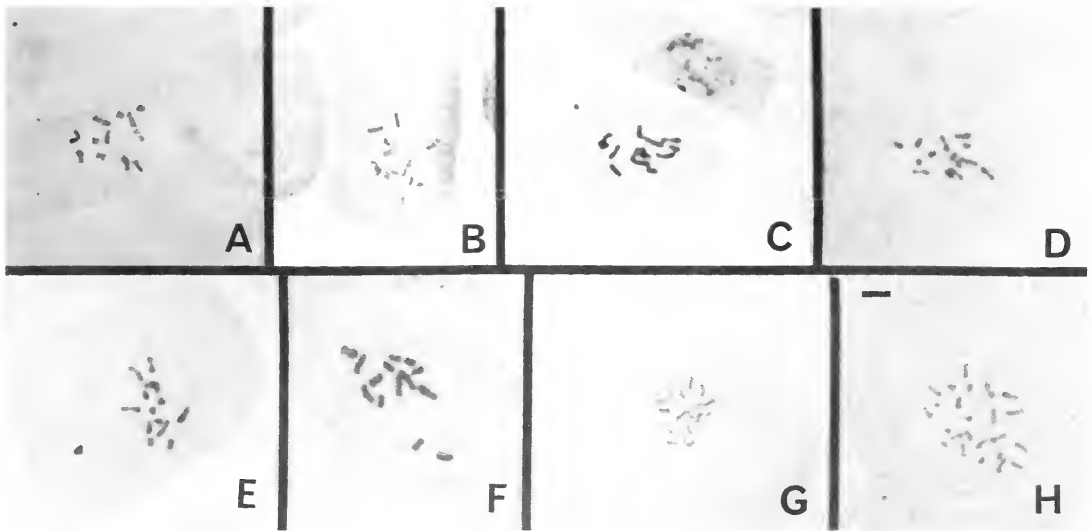


FIGURE 3.—Mitotic chromosomes in some *Lachenalia mutabilis* specimens. A, *Spies* 6751, $2n = 12$; B, *Spies* 6744, $2n = 12$; C, *Spies* 6760, $2n = 14$; D, *Spies* 6748, $2n = 14$; E, *Spies* 6757, $2n = 14$; F, *Spies* 6789, $2n = 14$; G, *Spies* 6749, $2n = 14$; H, *Spies* 6750, $2n = 24$. Scale bar: $6.5 \mu\text{m}$.

Lachenalia pustulata and *L. unicolor*: during this study somatic chromosome numbers of 38 *L. pustulata* specimens, representing at least 10 different localities, and 34 *L. unicolor* specimens, representing at least 12 localities, were determined (Table 2). All specimens were diploid with $2n = 2x = 16$ (Figure 4), except one *L. pustulata* specimen, *Spies* 6794, which was diploid (19 cells) and a single tetraploid cell was observed. This study confirms published reports on a chromosome number for *L. pustulata* (Johnson & Brandham 1997; Kleynhans 1997) and *L. unicolor* (De Wet 1957; Hancke 1991; Johnson & Brandham 1997; Kleynhans 1997).

The karyotypes of the two species correspond. Both species have four chromosomes that are significantly

longer than the other chromosomes. The chromosome numbers of the species are the same. In order to determine whether Duncan's (1988) suggestion of combining the two species is correct, meiotic chromosome behaviour of crosses between these species and pollen viability of the hybrids should be studied.

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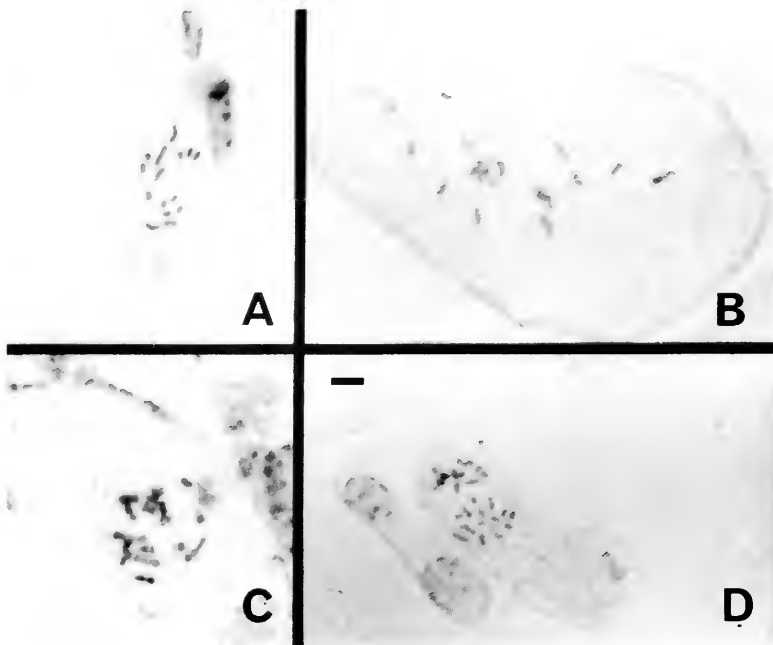


FIGURE 4.—Mitotic chromosomes in some *Lachenalia pustulata* and *L. unicolor* specimens. A, B, *L. pustulata*: A, *Spies* 6803, $2n = 16$; B, *Spies* 6798, $2n = 16$. C, D, *L. unicolor*: C, *Spies* 6838, $2n = 16$; D, *Spies* 6840, $2n = 16$. Scale bar: $6.5 \mu\text{m}$.

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OBITUARIES

LESLIE EDWARD WOSTALL CODD (1908–1999)

Leslie Edward Wostall Codd (Figure 1) was born at Vants Drift in KwaZulu-Natal on 16th September 1908. He matriculated at Dundee High School, and from 1925 to 1928 continued his studies at Natal University College, graduating in 1928 with an M.Sc. with a first class in botany. A year later he won the Webb Research Scholarship and continued his studies at Cambridge University, where he studied genetics under Professor Engeldon in 1929. In 1930 a Colonial Agriculture Scholarship took him to the Imperial College of Agriculture, Trinidad, where he worked on the genetics of cotton. He was employed as a plant breeder in the Department of Agriculture, British Guiana during the period 1931 to 1936. Here he met and married Cynthia Schneidersmann, a marriage which was to last for 65 years.

In January 1937 he joined the Pasture Research Section in the Division of Plant Industry, of the Department of Agriculture in Pretoria. Subsequently during 1939 he was appointed Officer in Charge of Prinshof Grass Breeding Station in Pretoria, a station concerned with the selection, growing and testing of pasture grasses. Four years later he obtained a D.Sc. degree at the University of South Africa, for a thesis on rice breeding.

In 1945 Dr Codd was appointed as Officer in Charge of the Botanical Survey Section in the Division of Botany, and remained stationed at Prinshof Experiment Station. This heralded the start of a career as a botanist spanning 28 years. During the time that he was in charge of the Botanical Survey Section and undertaking botanical collections (Figure 2) in the Northern Province, he became thoroughly acquainted with the flora of these areas, a knowledge which was to form the basis on which his later taxonomic research was founded. Plant collecting in the Kruger National Park culminated in his book *Trees and shrubs of the Kruger National Park* (Codd 1951)—one of the bestsellers in the *Memoirs of the Botanical Survey of South Africa* series. Several publications on ecological subjects appeared under his authorship during this period.

In 1951 the Division of Botany and Plant Pathology was split into two, namely the Division of Plant Pathology and the Division of Botany. In that year, following the retirement of Dr Inez Verdoorn, Dr Codd was placed in charge of the National Herbarium. In 1956 he was appointed Assistant Chief of the Division of Botany, which was later renamed the Botanical Research Institute. On Dr Dyer's retirement in 1963, Dr Codd was appointed Director of the Botanical Research Institute, a post he held until his retirement in 1973.

From the time of his appointment in the organization, Dr Codd was made responsible for the development of the Botanical Garden established by the previous director, Dr R.A. Dyer. For many years this project received his special attention. His constant support and encour-

agement, his interest and his live plant collections have contributed immensely to the growth of the Botanical Garden. Particularly during the period in which he was head of Botanical Survey, he was continually on the lookout for interesting and colourful plants which he collected and had grown in the Botanical Garden for painting and publication in *The Flowering Plants of Africa* series. In fact, Volume 43 of this series is dedicated to Dr Codd in recognition of this achievement and it records: 'His special interest in the development of the Pretoria National Botanic Garden, has contributed so much to South African Botany'.

During Dr Codd's tenure of office as Director, the BRI steadily grew. This is borne out by the fact that during 1966, following a public service inspection of the Institute, two new sections were created, namely a Flora Research Section and an Economic Botany Section. Further, a Plant Structure and Function Laboratory was created in 1969. The number of staff employed rose significantly during the following years.

The campaign for a new building, started by the previous Director, Dr R.A. Dyer, was vigorously promoted by Dr Codd, and in 1973, nearly 15 years after its initiation, a new milestone was reached when the Botanical



FIGURE 1.—Leslie Edward Wostall Codd (1908–1999).



FIGURE 2.—Dr Codd preparing specimens for pressing in camp, during the Bernard Carp Expedition to Barotseland, Zambia, August 1952.

Research Institute moved to the new building situated in the Botanical Garden.

As Director and Editor of the publications of the Botanical Research Institute, Dr Codd made significant contributions. Under his leadership, strength in scientific publications became a feature of this Institute. He personally provided the description of sixty-seven of the species depicted in *The Flowering Plants of Africa* series, eight of which were new to science. Plant groups which received his concentrated attention were, amongst others the genera *Albizia*, *Kniphofia*, *Erythrina*, *Schotia*, *Cassine*, the family Apocynaceae, and in later years, partly after his retirement, the family Lamiaceae. A large part of his research appeared in *Bothalia*, the house journal of the former Botanical Research Institute and of the present National Botanical Institute. His contributions to the *Flora of southern Africa* series are significant and cover the families Apocynaceae, Canellaceae, Loasaceae, the large family Lamiaceae and the genus *Cleome* (with L.E. Kers).

He possessed to a marked degree, that special gift, inherent in all successful taxonomists, of recognising and storing in his memory, the defining characters of plants and plant specimens and applying this knowledge to research. His taxonomic work has remained largely unchallenged and represents an extremely valuable contribution to South African botanical literature.

He also had the special gift of writing clearly, concisely and fluently with very little revision. This facilitated the work of the editorial staff, a fact commented on to me (B. de W.) on a number of occasions, possibly after receiving some of my own manuscripts.

His publications number 162 and include many taxa which were new to science. He is commemorated in the following: The genus *Coddia*, *Agapanthus coddii*, *Berkheya coddii*, *Brachystelma coddii*, *Erythrina* × *coddii*, *Eulophia coddii*, *Kniphofia coddiana*, *Lobelia coddii*, *Macrotyloma coddii*, *Rhus coddii*, *Tulbaghia coddii* and *Tylophora coddii*.

Dr Codd's contributions to Botany include plant collections numbering nearly 11 000 with many new records

and new species among them. His collecting has always been meticulous, particularly his labelling, and colleagues frequently stated that his field notes have often enabled them to return to the exact spot in the veld to find the plants from which he had collected. His extensive contributions in the form of live plant collections to the Pretoria Botanical Garden have already been mentioned. His main collection is deposited in the National Herbarium in Pretoria. Duplicates can be found in the Kew Herbarium, London, the Zürich Herbarium, Botanische Staatssammlung München, Geneva Herbarium and others.

Unlike many scientists, Dr Codd was an extremely helpful person, who was prepared to spend time to share his expertise with colleagues and other persons seeking advice. Numerous amateur botanists including Eve Palmer, Colonel Charles Scott and many other persons have benefited from his expertise. Very few of the botanical books published during the last two decades before the nineties appeared without some reference to encouragement and advice received by the authors from him.

Dr Codd played a major role in the affairs of scientific societies, becoming the president of several of them. He was intimately concerned with the establishment of the South African Association of Botanists, was a founder member and became its first president and an honorary life member. An active member of the South African Association for the Advancement of Science, he served on its Council for many years, ultimately becoming President of Section B (Botany) during 1957–1958. A strong supporter of the South African Biological Society, he made significant contributions, served on its Council for many years also as President in 1961 and was elected honorary member in 1985, the first to achieve this honour. As a long-standing member of the Botanical Society of South Africa he was elected honorary life member.

The excellence of his research was recognised in the awards of The South African Medal of the South African Association of Science in 1977, the Medal for Botany by the South African Association of Botanists in 1979, and the Senior Captain Scott Memorial Medal of the South African Biological Society in 1982. In December 1983

he was awarded an Honorary Doctorate of Science by the University of the Witwatersrand and in March 1990 an Honorary Doctorate by the University of Natal. In the eulogy preceding the latter award, he was described as: 'a gifted botanist, possessing a rare combination of qualities—acute perception and intuition, a disciplined scientific mind, painstaking thoroughness and a fine aesthetic sense.'

Dr Codd was an accomplished sportsman, played rugby for Cambridge and captained the Trinidad Rugby Team. He was a gentle person, full of humour, always fair, appreciative of work well done and a person it was a pleasure to work with and for. He genuinely appreciated the objects of his studies, and was quite prepared to delight in simple things. Many of his colleagues, staff and friends will recall anecdotes, most of them humorous, which they associate with him. Leo Jones, his technical assistant in the Prinshof days, was a great teller of tales, much appreciated by Dr Codd, who would laugh, in his special way, until the tears ran. One of us (B. de W.) remembers an early morning in the lowveld travelling on a sandy narrow track, hemmed in by tall grass, heavily covered with dew. Suddenly a francolin appeared in front of the car and waddled frantically down the road refusing to enter the wet grass to get out of the way. The movement of this little bird, very reminiscent of a fat lady running hard, was so ludicrous that we burst out laughing. For several hundred yards two grown men were laughing uproariously at a small bird! There was a special feeling between us that day. We had shared something simple and pleasant.

In his passing on the 2nd March 1999, botany has lost a special talent, but the legacy left behind is a life rich in contributions made in the pursuit of the knowledge of our plant environment.

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HUGH COLIN TAYLOR (1925–1999)

Hugh Taylor (Figure 3) was born in Simon's Town on 20 January 1925. In his youth he was strongly influenced by music and the natural environment. His father, Colin Taylor, was a musician and composer, formerly Music Master at Eton College, England and later a lecturer at the University of Cape Town School of Music. A love of music was passed on to Hugh who learned to play the piano. Hugh's mother was a member of the well-known Miller family after which Miller's Point was named. The Taylor family owned the farm 'Froggy Pond' at Simon's Town and a house known as 'The Shack' on the Cape Peninsula west coast in what is now the Cape of Good Hope section of the Cape Peninsula National Park. Hugh spent many weekends and holidays horse-riding and walking in these as yet unspoiled areas. His introduction to the fynbos and climbing the mountains thus came at an early age. These early influences set the tone for much of what was to happen in Hugh's rich and active life.

Hugh's mother Doris saw the need for conservation of the southern Cape Peninsula colloquially known as 'Cape Point' and she actively petitioned the authorities to proclaim the Cape of Good Hope Nature Reserve. The incorporation of this reserve into the recently proclaimed Cape Peninsula National Park bears testimony to the value of far-sighted actions to conserve areas of natural beauty and, as is well known, great plant species richness.

After matriculating at Rondebosch Boys' High School, he studied at the University of Stellenbosch, where he obtained a B.Sc. (Forestry) degree in 1946. Hugh then travelled abroad on a 'world tour' with his father, who was examining for the Royal Schools of Music. Hugh fondly remembered this trip with his father and always enjoyed travelling subsequently. In 1948 he joined the Department of Forestry and worked first as Assistant District Forest Officer, stationed at Bredasdorp, then in 1950–1951 as the District Forest Officer. From there he moved to Knysna where he was Forest Research Officer from 1952–1954. He then moved back to Cape Town in 1955 as District Forest Officer and married Dulcie Brooke-Smith in 1957. They lived briefly at Jonkershoek, Stellenbosch, where Hugh was again Forest Research Officer. In 1958 they moved to Pietermaritzburg where he held the post of Forest Extension Officer and Lecturer for two years at the University of Natal and at Cedara College. Their first daughter, Jennifer was born in Pietermaritzburg in 1959. It was during this period that Hugh became well acquainted with the Drakensberg by attending the Mountain Club of South Africa July camps. In 1960, Hugh resigned from

the Department of Forestry to attend the University of Cape Town where he obtained a B.Sc. (Honours) degree in Botany in 1961. It was in this year that their second daughter, Linden, was born in Heathfield, Cape Town. The Department of Agriculture then employed Hugh as fire ecologist at Stellenbosch (1962–1964) before being appointed to the Botanical Survey Section of the Botanical Research Institute in 1964. He then became the Officer in Charge of the Botanical Research Unit, Stellenbosch, in the same year, a post he held continuously till 1973.

The following excerpt from an article by C. Kavanagh in the January 14, 1955 edition of *The Outspan* epitomises Hugh's dedicated approach to Botany: 'When Mr Hugh Taylor, formerly of Cape Town, a learned young Forest Research Officer, took me through the forest (Knysna) I asked the obvious layman's question: "Why don't you patch with indigenous trees?" It turned out that this was asking for punishment, which I got. His reply



FIGURE 3.—Hugh Colin Taylor (1925–1999). Photo by Adela Romanowski.



FIGURE 4.—Hugh Taylor collecting vegetation data in a demarcated plot at Cape Point, 1966.

was a running lecture in foresters' language delivered during an afternoon of scrambling and slithering on steep forest paths, or forcing our way through ferns and brambles. We even came disturbingly near the bad-tempered Knysna elephants, but Mr Taylor lectured on. By sundown I felt that I had seen every tree in the forest, but had merely been taken to a few of the experiments in indigenous tree-growing begun by foresters as long as 50 years ago, and still incomplete.'

Hugh Taylor's survey methods were strongly influenced by John Acocks, the doyen of vegetation survey in South Africa whom he met in 1962. He accompanied Acocks in the field on a number of expeditions through the fynbos and elsewhere and was always amused by Acocks's formal manner. Acocks never failed to address Hugh simply as 'Taylor'! Following Acocks's example and later using other methods, Hugh conducted many formal and *ad hoc* surveys of the vegetation of the southwestern Cape. He developed an extensive knowledge of the fynbos flora as well as the forest flora of this region.

Hugh's roots drew him back to the Cape Peninsula, where his family had been allowed to retain 'The Shack' in the Cape of Good Hope Nature Reserve (The Shack was demolished in 1968). In the mid-1960's he initiated a survey of the vegetation of the reserve. The objective was to describe the plant communities for which he obtained an M.Sc. degree from the University of Cape Town in 1969. This survey formed the basis for a subsequent management programme for the vegetation of the reserve. It was during this time that Hugh's attention was drawn to the threat posed by alien invasive plants to the natural fynbos, both on the Cape Peninsula and elsewhere. He campaigned vigorously to bring the scourge of alien invasive plants to the attention of the public through a number of popular articles and his involvement in numerous 'hack groups'. He spoke often about the effects of alien vegetation on the fynbos of Red Hill above Simon's Town, where his mother and sister lived, an area he knew intimately.

The methodology used by Hugh Taylor for his Masters degree was based on Association Analysis. He

applied the method to the data he had collected from 100 samples laid out on a regular grid over an area of 78 km² in the Cape of Good Hope Nature Reserve (Figure 4). Upon completion of this work he travelled to Europe in 1971 where he spent nine months in Germany, studying under Reinhold Tüxen, a well-known phytosociologist who lived in Rinteln. Tüxen had in turn studied under the famous Joseph Braun-Blanquet after whom the now extensively used tabular method of sorting vegetation communities was named. While at Rinteln, Hugh and his wife Dulcie travelled to Montpellier in the south of France to meet Braun-Blanquet (Figure 5), a rare privilege for a South African phytosociologist.

The application of the Braun-Blanquet phytosociological method was a new introduction to South Africa at about the time Hugh returned from Germany. He collaborated with Marinus Werger, a phytosociologist visiting South Africa from Holland and employed by the Botanical Research Institute, and Fred Kruger of the Department of Forestry in a study of the vegetation of Swartboskloof, Jonkershoek, near Stellenbosch. The objective was to test the floristically based method in species-rich fynbos vegetation. The method proved to be successful



FIGURE 5.—Hugh Taylor with the esteemed J. Braun-Blanquet at Montpellier, France, 1971.

and became favoured as the most suitable one for studying not only fynbos but also for all other vegetation types in South Africa.

A few years after his return from Germany, Hugh was transferred to Pretoria for a brief period as Officer in Charge of the Botanical Survey Section (1974–1975), returning to his former position at Stellenbosch in 1976.

Hugh was a keen mountaineer and, even when climbing for pleasure he would often stop to consider an interesting plant or indeed do a 'plot'. Here he would make copious lists of plant species following the methods learnt from John Acocks. In the late 1970's Hugh conducted a study of the Rooiberg near Ladismith in the southern Cape. This gave him the opportunity to familiarize himself with the somewhat more arid fynbos flora so different from that found in the moister mountains of the southwestern Cape. This was to stand Hugh in good stead when he moved his research focus to the vegetation of the Cederberg.

Hugh published a total of 70 scientific and popular articles and papers and was always eager to inform people about fynbos, its diversity and conservation. In the early 1980's he served on the Steering Committee of the Fynbos Biome Project. The chapter entitled 'Capensis' written for the book *Biogeography and ecology of southern Africa* edited by M.J.A. Werger (1978) served well for this project as a benchmark paper for the state of knowledge of fynbos at that time. Hugh's meticulous records and personal knowledge gained over many years were in constant demand by researchers involved with the Fynbos Biome Project and he made a significant, if somewhat undocumented, contribution to the success of that project.

The Taylors left Stellenbosch in 1983 and moved to Clanwilliam to allow Hugh to be closer to the Cederberg which he loved and where he was to survey the vegetation for the next five years. During his stay in Clanwilliam, Hugh would ride up the rough mountain tracks of the Cederberg in a Land Rover (Figure 6) and when the tracks ended, would proceed on foot to his selected mountain survey sites. After toiling in the sun for hours, he would, after a light lunch, characteristically fill his pipe, smoke for a while and then have a nap under a nearby bush, tree or rock that offered a vestige of shade. Anyone working with Hugh soon became used to this post-prandial ritual! The half-hour snooze invigorated Hugh to carry on with his work for the remainder of the afternoon!

Hugh was always enthusiastic about conservation and he played an active role in the Cederberg Interest Group, established under the auspices of the Botanical Society of South Africa. He participated in the Cedar Restoration Project and was involved with WWF-SA in securing property at Matjiesrivier to form the Matjiesrivier Nature Reserve.

Hugh Taylor's definitive survey and classification of the vegetation of the Cederberg published as *Cederberg vegetation and flora*, a volume in the *Strelitzia* series of the National Botanical Institute is arguably his most

important contribution to understanding the montane vegetation of the Cape Floristic Region.

In 1990 Hugh and Dulcie retired to Froggy Pond, Simon's Town, a new suburb laid out on the farm of the same name which had belonged to the Taylor family. They took up residence in Dorrie's Drive, a road named after Hugh's mother! The circle was complete. But despite his retirement, Hugh found it hard to ignore his passion for the fynbos and the mountains. He travelled to Australia where he climbed in the Grampians in Victoria and then to New Zealand where he undertook a number of hiking trails with a long-standing friend. When at home, Hugh regularly walked on the Cape Peninsula Mountains and every so often in the Cederberg. His retirement allowed him more time for activities with the Botanical Society and Mountain Club of which he had an unbroken membership of over 50 years. He actively hacked alien vegetation on Red Hill above Simon' Town. Always interested in happenings around him, Hugh attended summer school courses at the University of Cape Town in his last years.

Hugh was a member of the following organizations: Botanical Society of South Africa, Dendrological Society, Endangered Wildlife Trust, International Association for Vegetation Science, Mountain Club of South Africa, South African Association of Botanists, South African Institute for Ecologists and Environmental Scientists, South African Institute for Forestry, and the Wildlife & Environment Society of South Africa.

Hugh collected about 12 000 well-documented plant specimens. Among these were a number of species new to botany and in many cases Hugh's records filled the



FIGURE 6.—Hugh Taylor in the Cederberg, 1983.

gaps in the distribution of many species. His collections formed an important part of the Stellenbosch Herbarium that was amalgamated with the Compton Herbarium, Kirstenbosch in 1996. Two species, a legume *Aspalathus taylorii* R.Dahlgren and a restio *Cannomois taylorii* H.P.Linder, commemorate Hugh's intimate involvement with the fynbos. His extensive collection of journals, reprints and original sets of data are housed in the Botany Department, University of Stellenbosch and his well-organized collection of colour slides is archived at the National Botanical Institute, Kirstenbosch.

Hugh contracted cancer that went undiagnosed for some time. He bravely fought the disease and looked forward to a recovery that was not to be. A little over a month before he took seriously ill, Hugh was up on the mountain at Red Hill, removing alien plants and walking amongst the fynbos that he dearly loved. While in hospital and in pain, with little hope of returning to an active life, Dulcie, Hugh's dear and compassionate wife, said to him that this would be the hardest mountain that he would ever have to climb, but that when he reached the top the view would be fantastic! Hugh died on the 6th July 1999 at Peers Village, Fish Hoek and a memorial service was held for him at St Francis Church, Simon's Town a week after his death.

Hugh Taylor will be fondly remembered by his family and many friends and acquaintances for his kind, caring nature and for being a true gentleman. He is survived by his wife Dulcie, daughters Jenny and Linden, Linden's husband Paul and three grandchildren.

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BARBARA JOAN JEPPE (1921–1999): BOTANICAL ARTIST EXTRAORDINAIRE

Barbara Joan Jeppe (née Brereton) passed away on 19 June 1999, following complications after contracting pneumonia. Although she was diagnosed with lung cancer in 1998, her condition improved substantially for about seven months, enabling her to complete a beautifully illustrated, large-format book on selected species and cultivars of iris (Jeppe 1999).

Barbara was born on 21 May 1921 in the small gold mining town of Pilgrim's Rest in the Mpumalanga Province of South Africa where her father was a land surveyor. At an early age she was introduced to wild flowers, pri-

marily through the efforts of her mother who taught her how to press them (Anon. 1999; Barron 1999). Her parents, Victor and Gladys Brereton, eventually moved to Johannesburg in 1928, where she matriculated some years later from Parktown Girls High School. During these years her love for nature, particular the flora, grew and blossomed. Her passion for painting flowers stayed with her for the rest of her life, even though she married at the young age of 20 and had a family to tend to. Four children, Leigh, Marie, Carl and David, all involved in the field of art, were born from her marriage to psychiatrist, Dr Carl Jeppe.

Some twenty-odd years after her wedding, she illustrated her first book, *Trees and shrubs of the Witwatersrand* (Tree Society of southern Africa 1964). This work established her career as a respected botanical artist and in the next 10 years it was followed by the books on the aloes of South Africa (Jeppe 1969) and the wild flowers of Natal (Jeppe 1975).

It was especially through her book on aloes that Barbara became well known amongst succulent plant enthusiasts and the popularity of the book ensured the production of updated editions in 1974 and 1977. The aloe books of both Jeppe and Reynolds (1950) were rapidly sold out and today any of the editions of both books are valuable Africanana, items affordable only by wealthy collectors. She also produced a little book on aloes for inclusion in the *Pride of South Africa* series (Jeppe 1974), which was available in hard and soft cover editions and was also translated into Afrikaans.

Barbara was not only good at painting aloes. She produced numerous beautifully illustrated books on a range of botanical topics, such as the wild flowers of Natal which included four striking plates of aloes (Jeppe 1975), and spring and winter flowering bulbs of the Cape (Jeppe 1989; Pretorius 1989). Even though she preferred delicately detailed watercolours, she also illustrated a couple of books on, for instance, acacias (Davidson & Jeppe 1981) and cycads (Giddy 1984) by using pencil and pen and ink drawings.

The winter rainfall area of South Africa is home to one of the richest, most diverse and colourful bulbous floras in the world. Barbara's book on Cape bulbs (Jeppe 1989) includes watercolours and descriptions of 420 species, subspecies and varieties from this unique flora. Many of these bulbous inhabitants have, until Barbara Jeppe filled the void, been rather poorly known except to a handful of specialists. Although she had never studied either botany or art formally, the illustrations and text show her acute powers of observation, technical correctness and precise attention to detail.

It has been said that Barbara Jeppe's work is distinguished by an exceptional sense of colour. Her amazing ability to capture the elegance and beauty of plants in exuberant colours and also reproduce them with scientific accuracy led to her participating in projects such as Ciba-Geigy's (1975) illustrated handbook, *Effective weed control in maize and grain sorghum*. The book that contains 32 of her watercolours, today still serves as an authoritative guide to the identification of weeds commonly occurring with these crops in the field (Grabandt 1975). Moreover, it created an enormous demand from naturalists, agriculturists and horticulturists for a more comprehensive work. Consequently, Ciba-Geigy (1985) sponsored another publication, *Weeds of crops and gardens in southern Africa*, containing 134 full colour reproductions of paintings: 91 by Barbara Jeppe and 43 by Swiss artists from the Zürich School of Applied Art.

Sadly, Barbara did not live to see the publication of her iris book by Umदाus Press, Pretoria, which was launched on 24 August 1999 only some two months after she passed away. In many respects this was one of her finest



FIGURE 7.—Barbara Jeppe with a potted specimen of *Strumeria barbarae* Oberm. (Amaryllidaceae), the plant that was named in her honour.

productions. Barbara did not know much about irises when she started on the project, but true to her personality, she set about it with typical enthusiasm. The iris cultivars and species were painted with exceptional accuracy and in large format—the dimensions of the book are 420 × 297 mm portrait—with minute detail paid to the shape and colour of these striking Eurasian and North American garden plants. Although they are not indigenous to southern Africa, they are exceptionally versatile as garden subjects and have become so entrenched in local amenity horticulture that few gardeners give a second thought to the fact that they hail from foreign shores (Anon. 1982; Gardiner 1990). Indeed, in the words of Steve Bales, who wrote the foreword to the iris book (Jeppe 1999: 7), '...there certainly must be at least one (iris),...which will seduce the indigenous purist to set aside a suitable garden bed in which these plants may make their home'.

Another project in which she was involved will only be published posthumously, namely the one on the Amaryllidaceae of southern Africa. The text of this grandiose project is being written by Dr Piet Vorster of the Botany Department of the University of Stellenbosch. As with her previous works it is sure to be illustrated prolifically with her excellent paintings such as the *Clivia miniata* plate reproduced here (Plate 1).

A species of the family Amaryllidaceae, *Strumeria barbarae*, was named after her in 1981 (Figure 7). For her input to botany and horticulture she was awarded two



PLATE 1.—*Clivia miniata* (Lindl.) Regel, one of numerous Amaryllidaceae painted by Barbara Jeppe.

gold medals in 1990, one by the Botanical Society of South Africa—the Cythna Letty Gold Medal for contributing to botanical illustration in South Africa—and another by the South African Nurserymen's Association. The Transvaal Horticultural Society bestowed on her a silver medal in 1991.

We mourn the passing of an accomplished botanical artist who contributed extensively to popularise the magnificent flora of southern Africa.

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Book Reviews

DIE INFLORESZENZEN. TYPOLOGIE UND STELLUNG IM AUFBAU DES VEGETATIONSKÖRPERS. Zweiter Band Teil 2: Monotele und polytele Synfloreszenzen, by F. WEBERLING. 1998. *Gustav Fischer Verlag Jena*, Villengang 2, D-07745 Jena, Germany. Pp. 483. Hard cover: ISBN 3-437-35436-1, price DM 238, ÖS 1737, SFr 211.

This latest volume now completes the study of the morphology of the angiosperm inflorescence begun more than 50 years ago by the great German morphologist Wilhelm Troll and continued by his disciple Focko Weberling. The previous two books in the trilogy are Troll 1964 & 1969, vol. 1 and vol. 2, part 1 respectively.

Numerous excellent line drawings, diagrams and photographs (totalling 474) encourage the reader not well versed in German to decipher the text. For those students of botany who have missed out on a German translation course at university, I would suggest starting with another book by the same author: Weberling 1988, *Morphology of flowers and inflorescences*. This is a meticulous translation from the German by R.J. Pankhurst and has a good glossary. Weberling provides the basis for the typology of the inflorescence and distinguishes between the monotelic and polytelic synflorescences (synflorescence: a system of inflorescences).

This final volume deals with the monotelic synflorescences present in the families Rubiaceae, Asclepiadaceae, Polemoniaceae, Convolvulaceae and Campanulaceae, followed by the polytelic synflorescences of the Leguminosae, Lamiaceae, Scrophulariaceae and Plantaginaceae. There is a taxonomic index to all genera and species covered in the last two volumes, as well as a general subject index. This should provide easy access to the serious student and to the systematist having to describe the great diversity of inflorescences found in a particular family or even genus.

As a palaeobotanist I was particularly interested in chapter 5, part 4, *Zur allgemeinen Phylogenie der Infloreszenzen*, i.e. Towards the general phylogeny of the inflorescences. However, this chapter is extremely brief (which I found disappointing). In it Weberling refers to the ideas of Parkins (from 1914) who regarded the flower as originally borne singly and terminally on a leafy shoot. This is the pattern occurring in many of the Magnoliales and in some of the early angiosperm flowers from the mid-Cretaceous, e.g. *Lesqueria* and *Archaeanthus*. However, from rocks of the same age, small simple flower types, similar to those of some Chloranthaceae and Platanaceae, have also been found. I suspect that in the long term the answers to the phylogeny of the flower and inflorescence will come from the fossil record. Angiosperms, as we now know them, are the end result of over 100 million years of evolution. During that time they evolved into the mind-boggling diversity of today. While DNA studies may provide clues, it is the earliest fossil angiosperms that are the key to angiosperm phylogeny. So what is needed urgently, is not only more scientists to describe and understand the present plant diversity which is in serious decline through habitat destruction, but more palaeobotanists to carry out extensive collections in an effort to find further early angiosperms and their progenitors.

The book and its companion volumes provide a valuable tool for understanding and describing the inflorescences of angiosperms and constitute essential reference works for all botanical libraries as well as for many plant taxonomists, morphologists and other botanists.

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FIELD GUIDE TO THE ACACIAS OF ZIMBABWE, by JONATHAN TIMBERLAKE, CHRISTOPHER FAGG & RICHARD BARNES. 1999. Illustrations by Rosemary Wise. *CBC Publishing*, P.O. Box 4611, Harare, Zimbabwe. Pp 160. Soft cover: ISBN 0-7974-1936-5, price GBP 7.50.

Several works on southern African acacias have been published over the past number of years (Brenan 1970; Ross 1975; Carr 1976; Ross 1979; Davidson & Jeppe 1981; Steyn 1994; Smit 1999), so one asks the question, 'why another one?' The authors feel that there is a need for an everyday identification guide to the some 40 species found in Zimbabwe, more particularly for use by people concerned with land management, whether agriculturalists, wildlife managers or interested naturalists. Some of the species covered reflect soil type and land potential, some are of significant economic value for fuel, browsing, fencing and other products such as gum, while others have great potential for improvement of degraded land.

This publication emanated from a research project conducted over the last decade by Richard Barnes and Christopher Fagg of the Oxford Forestry Institute, in association with Suzanne Milton. The results of range-wide studies of the distribution, ecology, taxonomy and variation of African *Acacia* species were used to compile two comprehensive monographs on *Acacia karroo* and *A. erioloba*. These studies were funded by the United Kingdom Department for International Development for the benefit of developing countries. Jonathan Timberlake from the Biodiversity Foundation for Africa, Bulawayo, Zimbabwe co-authored this publication with Richard Barnes and Christopher Fagg.

The cover has a clever fold-out feature: the front cover folds out to reveal a full colour map of Zimbabwe; the inside back cover contains a quick identification table of the species described. The introduction deals with various important subjects such as Taxonomy, Origin and Distribution, Ecology and Uses. Acacias in vegetation, plant succession, bush encroachment, rooting habits, nitrogen fixation, animals and acacias, edible products and medicines, are some of the subjects discussed.

The following part deals with the description of the different *Acacia* species and highlights the various characteristics such as life form, trunk and bark, young twigs, thorns, leaves, glands, flowers, pods and seeds. This is followed by a detailed description on 'how to use this field guide'. It incorporates four different methods to identify a specimen, either by means of the illustrations, distribution maps, descriptive text or one of the three keys provided.

The dichotomous key is based mainly on vegetative characters and incorporates pods and flowers only where deemed necessary. It also helps the identifier to distinguish between *Acacia* species and similar-looking non-acacias, such as species of *Albizia* and *Dichrostachys* as well as Australian acacias. The other two keys are different types of character matrices. In the species matrix on the inside back cover of the book, any of the readily noted field characters are shown. A solid circle signifies that the character is nearly always present; an open circle signifies that the character is only occasionally present. The character matrix on p. 22 lays out a selection of easily noted vegetative characters along the top axis and inflorescence and pod characters along the vertical axis. Any species with that combination of characters is mentioned where the column and row intersect.

Descriptions of 40 species found in Zimbabwe are provided and arranged alphabetically. These are concise and to the point, with important characters highlighted in bold, based on Zimbabwean specimens and field notes. The common names for each species are also given in languages used in Zimbabwe. The major field characters are listed after the main description. This is followed by details on characters differentiating the species from others with which it might be confused. For each species a distribution map is provided, with distributional notes compiled from herbarium specimens available from numerous herbaria throughout Zimbabwe, the Royal Botanic Gardens at Kew, Forest Herbarium at Oxford and the National Herbarium in Pretoria, as well as ecological notes primarily derived from the authors' own field observations. The final section under each description includes notes on the general biology, the nomenclature of the species and its various economic uses gained from local literature and local observations.

Illustrations are provided in the form of Rosemary Wise's excellent line drawings of the habit, thorns, leaves, leaflets, glands, inflorescences, fruit and seeds. These illustrations are so accurate that it is often not necessary to refer to the accompanying descriptive text to identify an *Acacia* species. The height of the trees can readily be gauged by comparison with drawings of all kinds of human or animal figures under the tree or even by a parked vehicle, rendering a humorous touch to the illustrations. Furthermore, the illustrations and maps are conveniently placed near the relevant text.

Included in the latter part of the book are illustrations of pods from all indigenous acacias, grouped under spicate and globose flowered species. There is also a list of species found in various geographical regions and vegetation types in the country, as well as a glossary of botanical terms used, some of which are illustrated, a list of common names, a comprehensive bibliography of sources of information used in the preparation of the book and finally an index of all scientific names.

I can recommend this guide without hesitation to acacia enthusiasts throughout southern Africa, particularly since it covers an area containing species not found elsewhere. An added bonus is its light weight and A5 size, facilitating easy handling in the field.

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The author has taken into consideration that the users of the book may not all be experts and consequently described the plants in simple terms, in many instances using descriptions of other objects to explain the structure. For example, the hairs occurring on the adaxial surface of the leaves of *Salvinia molesta* were described as looking like an egg beater and when observed under the microscope, the description is seen to be very apt. The keys are very user friendly and when using them it soon becomes clear that they have been compiled by someone very knowledgeable who can also stress their diagnostic characters. The 374 excellent illustrations, which were all done by the author, conveniently occur on the same page as the descriptions, thus eliminating the necessity of having to page to and fro. In addition, the clear, concise diagrams enhance the descriptions as well as facilitate comparison of different species. Moreover, in many instances it can be used as a glossary to describe terms used in other publications. There are 67 families with 187 genera and 685 species dealt with in this book, of which 62 species occur in both South Africa and India. The description is followed by reference to a current publication, the habitat of the plant, distribution in India and elsewhere in the world and some interesting general information. There is a map of the Indian subcontinent showing the area covered in this book. The distributions within India are represented by symbols in respect of each province. This, however, I find somewhat irritating having to continuously refer to the map in the front of the book to ascertain where the plant occurs. A small map showing the distribution of each species, or at least the more common ones would have been preferable. However, considering the time it would have taken to compile these maps, it would not have been possible to produce such a document in the time available. Even though genera such as *Largarosiphon* and *Hydrostachys*, which only occur in Africa and Madagascar, as well as some of the genera in the family Podostemaceae, and *Prionium* which is endemic to the southern part of Africa, are of course not mentioned in this book, it is still highly recommended to anyone doing research on this group of plants in southern Africa.

In his review of this book, Donald H. Les said: 'So, those are my criticisms which one can clearly see are relatively minor. None of them detract in the least from this otherwise outstanding taxonomic coverage of Indian aquatics which will undoubtedly become another classic in water plant literature. Christopher Cook is good at writing such classics and we only hope that now that he has the flora 'bug', he will continue to use his extraordinary abilities to make taxonomic sense of water plants from other regions. Hmmm. I don't think that Africa has a comprehensive aquatic flora yet.'

Prof. Cook indicated in his Preface that this book would be his final contribution before going into retirement. He briefly visited South Africa towards the end of last year. A few of us, namely Roddy Ward, Mike Coke, and myself, were fortunate enough to show Prof. Cook some of the aquatic plants that occur in KwaZulu-Natal. Fortunately the 'flora bug' has bitten this renowned aquatic botanist once more, and the *Aquatic and wetland plants of India* will certainly not be his 'last fling'. Currently Prof. Cook and the National Botanical Institute are involved in a joint project on the southern African aquatic flora.

Due to the ruling rate of exchange here in South Africa, the publication is fairly expensive for a book on flora not directly related to our country. Nevertheless, this book is far more than just a study on a flora of a specific country and I certainly recommend its use as a well-illustrated reference book on aquatic and wetland plants.

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AQUATIC AND WETLAND PLANTS OF INDIA by C.D.K. COOK, 1996. *Oxford University Press*, Oxford, UK. Pp. 385, A4. Hard cover. ISBN 0198548214, price approx. R1 200,00 (stocks limited).

This flora of wetland plants in India is the third book written by Prof. C.D.K. Cook on aquatic plants. *Water plants of the world* (Cook *et al.* 1974) and *Aquatic plant book* (Cook 1990) contain keys to all the genera of aquatic plants throughout the world. Even though most of the species in this book differ from those on the African continent, it is still a very useful reference book for any one doing research on aquatic plants in southern Africa.

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